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A HYBRID SWARM IN *JUNIPERUS*

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INTRODUCTION

The recognition of juniper populations of extreme heterogeneity in central Texas and southern Oklahoma initiated a detailed study of the comparative morphology of the constituent individuals. It was soon apparent that a study of the local species *Juniperus Ashei* Buchholz (*Juniperus mexicana* Spreng. of Gray's Manual of Botany, 8th Edition) and *Juniperus virginiana* L. in their entire distribution was essential. These two very distinct species occur together with abundant intermediates in scattered populations from Bexar County, Texas, to Ozark County, Missouri. A general survey of *Juniperus* east of the Rocky Mountains based on studies of population samples and herbarium specimens was made and has been published elsewhere (Hall, 1952).

Fassett (1944, 1945) had already "broken ground" through his variation studies at the northwestern and northern edge of distribution of *J. virginiana* in which he discussed the effects of hybridization between *J. virginiana, Juniperus scopulorum* Sarg., and *Juniperus horizontalis* Moench., on the integrity of these species. In his variation studies Fassett was working with one of the most difficult problems in American junipers, for the two former species are so very similar that Englemann (1877) considered them as one. Fassett reported the occurrence of hybrid swarms of *J. virginiana* and *J. horizontalis* on the east coast of Maine and in the Driftless Area of Wisconsin, of *J. virginiana* and *J. scopulorum* in central and southwestern South Dakota and northwestern Nebraska, of *J. scopulorum* and *J. horizontalis* in the Big Horn Mountains and near Banff.

Whiting (1942) reported bizarre recombinations of characters of *J. scopulorum* and *Juniperus pachyphloea* Torr. as exhibited by individual junipers growing in Oak Creek Canyon near Flagstaff, Arizona.

I know of numerous regions in the Southwest where hybrids between two species of junipers are quite common, and in one interesting area, the Palo Duro Canyon of the Texas Panhandle, there is a great mass of variable junipers among which four recognized species may be salvaged. Hybrid swarms are very common in the genus, and they usually cover quite extensive areas, *e.g.*, the region along the Balcones Escarpment in central Texas and the White River region of Arkansas and Missouri. From some of these hybrid swarms one may trace the

flow of genes from one species into the other for great distances but in progressively greater dilutions. Introgressive influence of *J. scopulorum* into *J. virginiana* and *J. Ashei* into *J. virginiana* is measurable over a distance of close to a thousand miles. Because of the focal point occupied by the hybrid swarms, extensive study of them was undertaken. Detailed data have been collected from a number of hybrid swarms of *J. virginiana* and *J. Ashei* from the Edwards Plateau of central Texas to the Ozark highland. This paper consists of a report on one of these hybrid swarms.

The Habitat

The hybrid swarm in question is situated near the southern edge of the Arbuckle Mountains in the vicinity of Platt National Park, Murray County, Oklahoma. Along the southeast boundary both within and without the park, there is an area covered with little-bluestem-grass and a few hundred junipers. These junipers are growing on rolling hills composed of the calcareous Pontotoc conglomerate. A small spring-fed creek and its tributaries drain the area. The general region with a 36-inch annual rainfall is classified as oak-hickory savannah by Bruner (1931), but actually the distribution of vegetation in the Arbuckles is fairly complicated principally because of edaphic complexities. The water relations in the Arbuckle residual soils are complicated by lithological factors, particularly by the presence of mosaics of markedly different rock strata. The vegetation reflects some of these lithologic differences. The Arbuckles are really a dissected upland (1,350 feet at the highest point and 750 feet at the lowest) showing a basal mountainous structure. From the heart of the upland outward, sedimentary deposits from upper Cambrian to Pennsylvanian age are exposed. The paleozoic formations of the Arbuckle Mountains represent upturned, beveled-off strata which before mid-Carboniferous time were 12,000 feet of horizontal strata.

In the Arbuckles, throughout the areas where junipers are growing, the hybrid swarms are found in the intermediate habitats. These hybrid populations are best developed on the slopes and in the small valleys of the undifferentiated limestones, sandstones, and shales characteristic of the Pontotoc conglomerate. The southwestern species, *J. Ashei,* occurs in the most xeric areas suitable for junipers. At the northeast limb of the Arbuckle anticline, four miles south of Davis, Oklahoma, the Viola limestone occurs on edge and is bordered by the Simpson formation on one side and by the Sylvan shale, Hunton beds, and Woodford chert on the other. The rounded limey knobs of the Viola are covered with grasses, dotted with *J. Ashei,* and a few widely scattered shrubby trees such as *Cercis canadensis* var. *texensis, Celtis laevigata* var. *texana,* and *Quercus breviloba.* The juniper in the Viola limestone is nearly equivalent morphologically to *J. Ashei* of the Edwards Plateau in south-central Texas. Likewise, the dry sparsely covered hilltops of the Pontotoc conglomerate support numerous stands of *J. Ashei.*

The variable Simpson formation supports grassland and oak woodland, depending on the presence of limestones and shales, or sandstones respectively in the surface material. The Sylvan shale supports an open oak savannah interrupted by xeric pasture ridges on the limestones of the Hunton beds which in turn are bordered by closed mixed woods on the Woodford chert. In the open areas of the woodland on these formations, specimens of *J. virginiana* may be found in considerable numbers. They are representative of the Ozark race of Red-cedar, being more variable, especially in habit, than the eastern race of *J. virginiana.*

Differential selection of genotypes is clearly evident in the Arbuckle Mountain junipers and in particular where hybrid swarms cross a lithologic boundary. The somewhat variable junipers on the Viola formation and on the hilltops of the Pontotoc formation are introgressants very close to typical *J. Ashei*; those plants on

the less xeric slopes and in the valleys of the Pontotoc conglomerate are intermediate and represent a hybrid swarm; and, finally, the junipers in the wooded areas are introgressants toward *J. virginiana* and are characteristic of the "Ozark race."

After one is familiar with the region and knows what has happened to *Juniperus* there, it is a simple task to describe the habitat, even to designating the geologic formation to which its substratum belongs, by the pattern of variation expressed by the juniper populations growing in it. The variation pattern of the junipers gives data similar to those obtained by plant sociological means. While such data do not establish a quantitative evaluation of the physical factors of the environment, they offer a dependable means of comparing habitats by comparing either population spectra or sociological spectra within them.

It is evident that habitat comparison based on population spectra is useful only in special cases, in which one has detailed knowledge of species or complexes in a bipolar relationship, for example, introgression between two rather different allopatric species. Without strong differential selection within the group in question, this technique would be useless. Also, as an initial characterization of habitat, it is useless, for one must already have the population patterns before comparisons may be made. For these reasons sociological surveys, which may be made initially and for any kind of population study, are best for establishing habitat similarities and differences. A detailed analysis of the effects of differential selection on population structure will be reported in a later paper.

Review of Morphology

At this point it is desirable to review the morphological differences between the species *J. Ashei* and *J. virginiana*. The comparative morphology of these species is discussed in detail in another paper (Hall, 1952).

The following table summarizes the major differences between the two species.

Juniperus Ashei	*Juniperus virginiana*
1. Trunk more or less branched near the base; aspect generally bush-like; height to 35 feet.	1. Trunk single, erect; aspect generally pyramidal; height to 80 feet.
2. Foliage dense.	2. Foliage more or less open or plume-like.
3. Foliage yellow-green.	3. Foliage bluish-green.
4. Glands on leaves uniformly round; raised well above the leaf in a convex hemisphere.	4. Glands much elongated on certain leaf types, elliptic on others; seldom raised above the leaf.
5. Fruit large (6–8 mm. in diameter) with slightly resinous juicy pulp.	5. Fruit small (3.5–5 mm. in diameter) with strongly resinous dry pulp.
6. Seed 4–5 mm. in diameter, 1, rarely 2 per berry-cone, sharply pointed tip, no pits, smooth white hilum conspicuous, covering at least one-fourth the length of the seed.	6. Seed 2–3 mm. in diameter, 1 or 2 per berry-cone, rarely 3–6, blunt tip, numerous pits, small inconspicuous hilum.

These two species are in different species groups within the Section *Sabina*. They are so different that they constitute opposite "poles" within the section. In technical characters *J. Ashei* is monospermous with denticulate leaf margins, while *J. virginiana* is polyspermous with entire leaf margins. *J. Ashei* grows as a large multi-stemmed or bushy xerophyte in subhumid to semi-arid environments, while the arborescent *J. virginiana* may grow in humid lowlands as well as drier uplands in the deciduous forest and prairie formations. *J. Ashei* grows only in calcareous soils or rock detritus while *J. virginiana* as a whole does well on calcareous material but is not restricted to it. The northern type of Red-cedar, containing the *crebra* element, is arenicolous but not obligately so.

Figure 1 shows the basic habit, branching system and leaf characters in these junipers. From the axis to the ultimate branchlets, branching continues to the

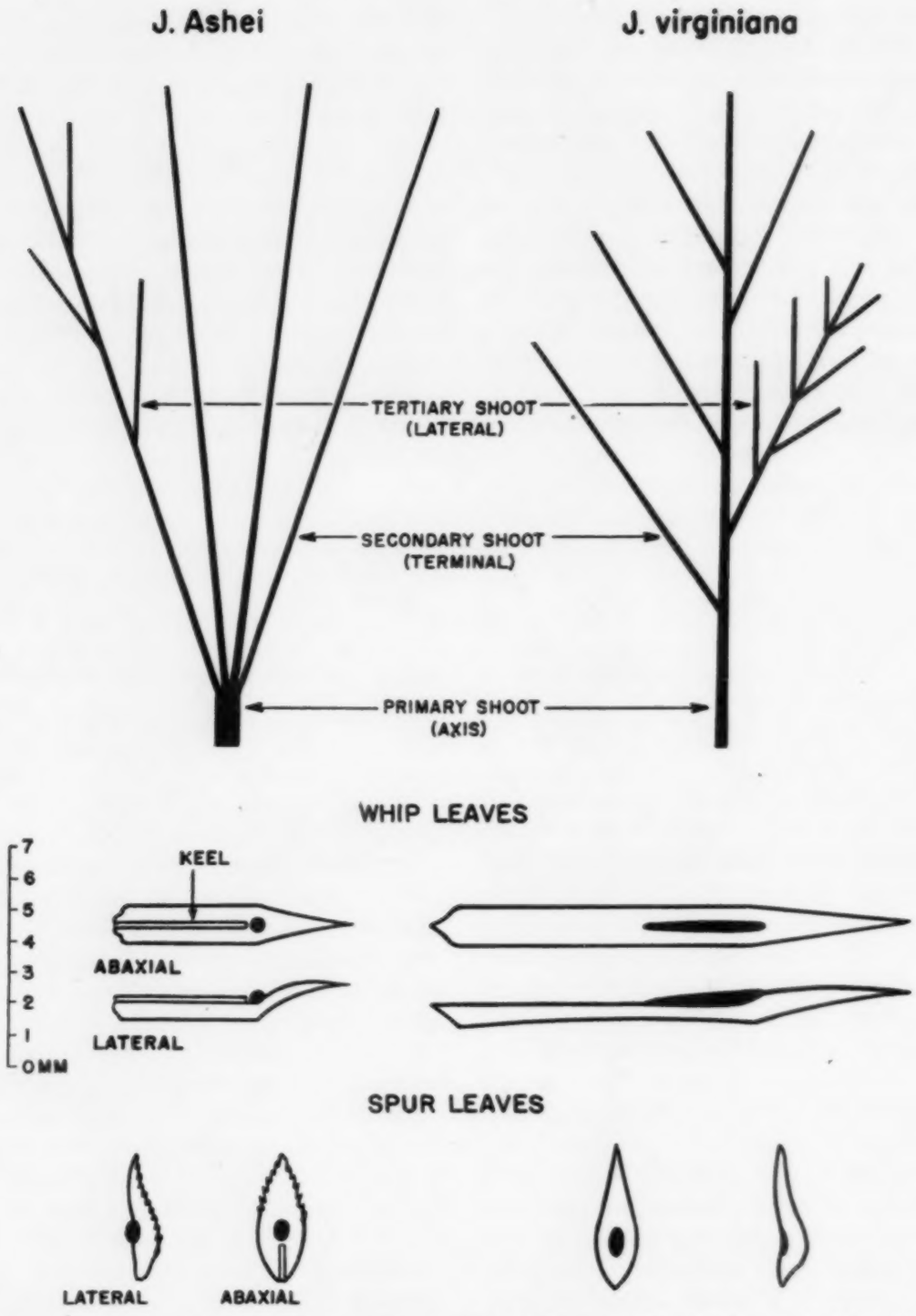

FIG. 1. Basic habit, branching system and leaf characters in *Juniperus Ashei* and *Juniperus virginiana*.

sixth degree in *J. virginiana* and the seventh degree in *J. Ashei* but is not represented in the diagrams beyond the tertiary. The leaf characters in figure 1 represent typical examples of *J. Ashei* and *J. virginiana* (Eastern race) and may be compared for structural similarity to the leaf characters of the hybrids in the photographs (figs. 8 through 11). The long leaves in figure 1 are whip-leaves characteristic of long-shoot growth which occurs terminally on secondary and tertiary

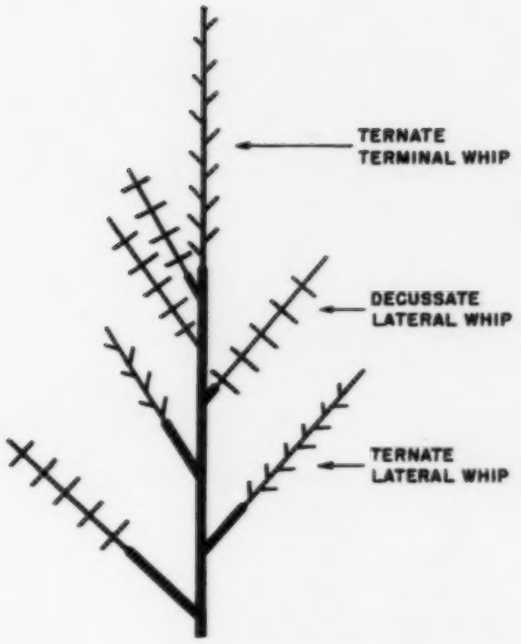

FIG. 2. A secondary shoot of *J. virginiana*.

shoots. The short leaves are spur-leaves characteristic of short-shoots.

Figure 2 is a diagram to scale of a secondary shoot twenty inches in length, showing its morphology and identifying the terminology used with respect to it in this paper. Terminal whip is the long-shoot growth which is characterized by long type leaves and borne at the apex of the secondary shoot. Lateral whip is long-shoot growth at the apex of the tertiary shoot or a major lateral branch (third degree of branching). The whip may have leaves arranged in a ternate or decussate pattern. Leaf arrangement shows up well in the photographs, figures 8 through 11. The spur-leaves of Number 8, figure 9, and Numbers 19 and 21, figure 11, are clearly decussate.

METHODS

The Population Sample. In the hybrid population from the Pontotoc conglomerate the individual junipers vary discordantly one from another to a degree easily observable from the roadside. Discordant variation is best comprehended by studying figures 3 through 7. The term is used in the same sense as by Anderson (1950) in his analysis of concordant and discordant variation in the hypothetical genus *Planta*. Discordance in morphological characters, gross habit, branching, size patterns, internode lengths, and ratios in other structures is the result of the mixing of unlike but somewhat miscible elements through hybridization. When multiple factors are shuffled, resulting in new combinations of genes and modifying factors, a heterogeneous population is the outcome.

A number of questions came to mind as I examined these populations which were so full of disharmony. Is there intra-individual as well as inter-individual discordance? What are the trends of character correlations in these populations? I wanted to find some repeatable way to typify a whole population by sampling a reasonable number of its constituent individuals. If the variation from branch to branch was slight within an individual plant, then a single branch from a comparable part of each tree might be collected and used as an index of the variability among individuals. One may determine the nature and relative degree of inter-individual variation by sampling comparable branches of a single plant and holding them in silhouette to the sky. When branches from different trees are compared, it is easy to get a relatively accurate idea of the degree of difference between branches of separate trees and that between the branches of a single tree. The branches of separate trees can always be sorted from one another while those from a single tree cannot be so categorized. The variability of the branches within an individual is sufficiently slight that one may typify a single plant by collecting a main branch or secondary shoot. The reliability of the secondary shoot for sampling was checked by comparing the various technical characters from branch to branch and tree to tree. Again, the tree to tree data could be sorted without the slightest difficulty, while the branch to branch data for single trees could not be clearly distinguished. In other words, the variation in separate individuals within the popula-

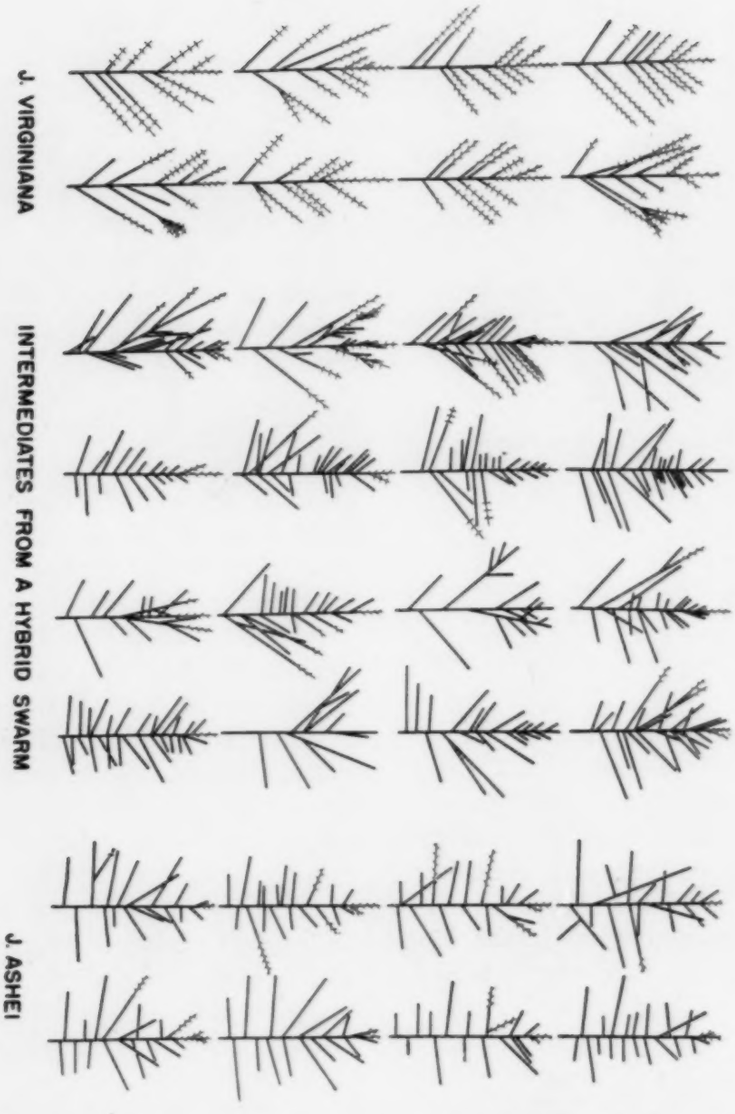

FIG. 3. Variation in branching pattern of typical *J. virginiana* (the two top rows), intermediates from a hybrid swarm (the four middle rows), and typical *J. Ashei* (the two lower rows). Compare with Fig. 2 for legend.

tion was of a different order from that between separate branches within the individual. The habit differences from tree to tree were accompanied by technical differences in every character studied. Next, it was necessary to determine the way in which these characters were correlated. Such pattern data could indicate whether the variations could be explained satisfactorily in terms of environmental fluctuations or in terms of hybridization—recombinations of characters.

The effect of environment on the several characters measured was also checked by examining a number of horticultural varieties of Red-cedar in widely spaced localities, *e.g.*, Texas, Oklahoma, Missouri, and Michigan. These populations were analyzed and five characters chosen with which to construct pictorialized scatter diagrams. Three of these diagrams have been published in an earlier paper (Hall, 1952, see populations 52, 53, and 54, page 52). There is little evidence that the characters are subject to modification, but rather, that they are under strong genic control.

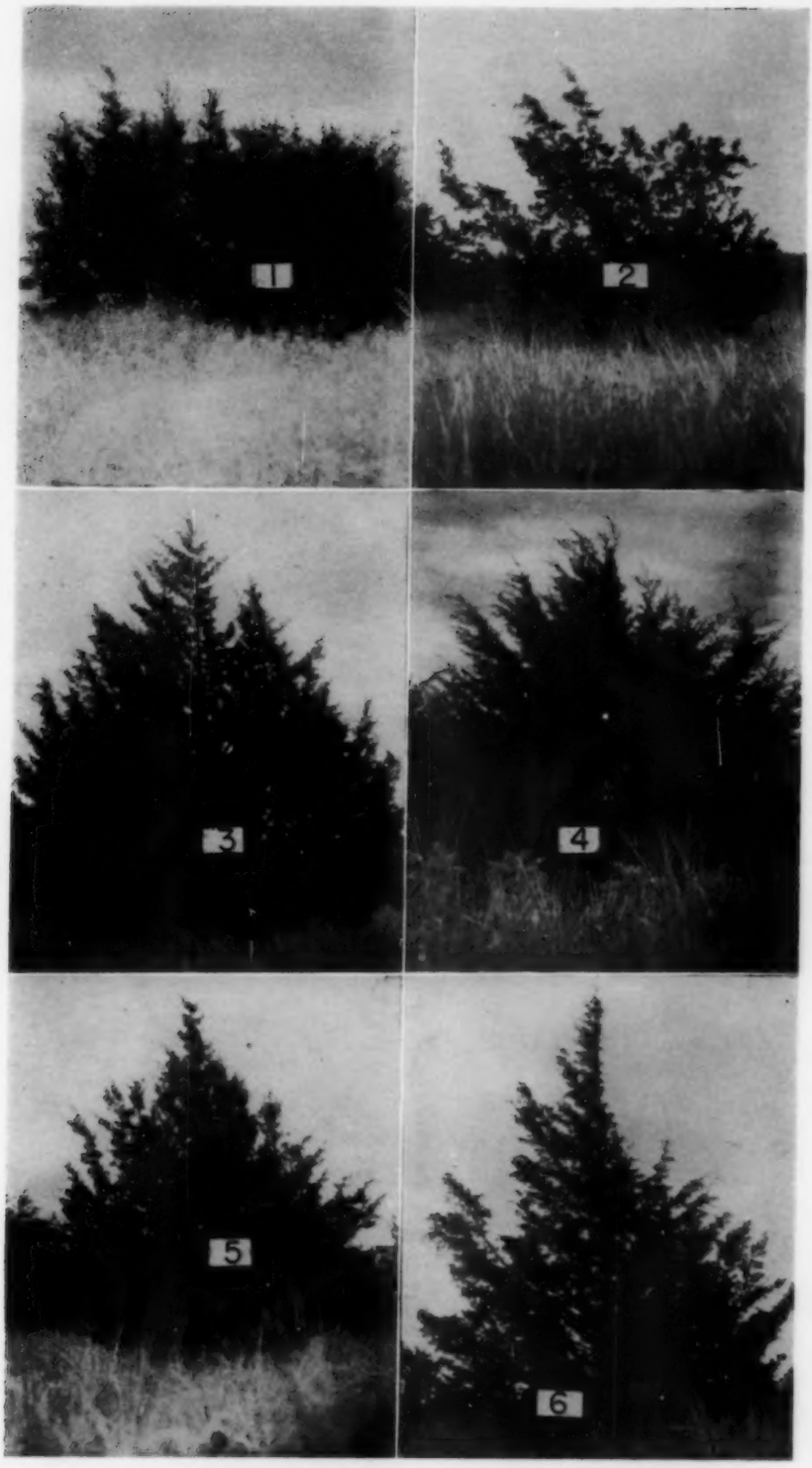

FIG. 4. Variation in habit—Figs. 4 through 12 represent a random collection from a hybrid swarm (*J. Ashei* and *J. virginiana*) at Platt National Park, Oklahoma. Number card is 1 foot on the vertical edge.

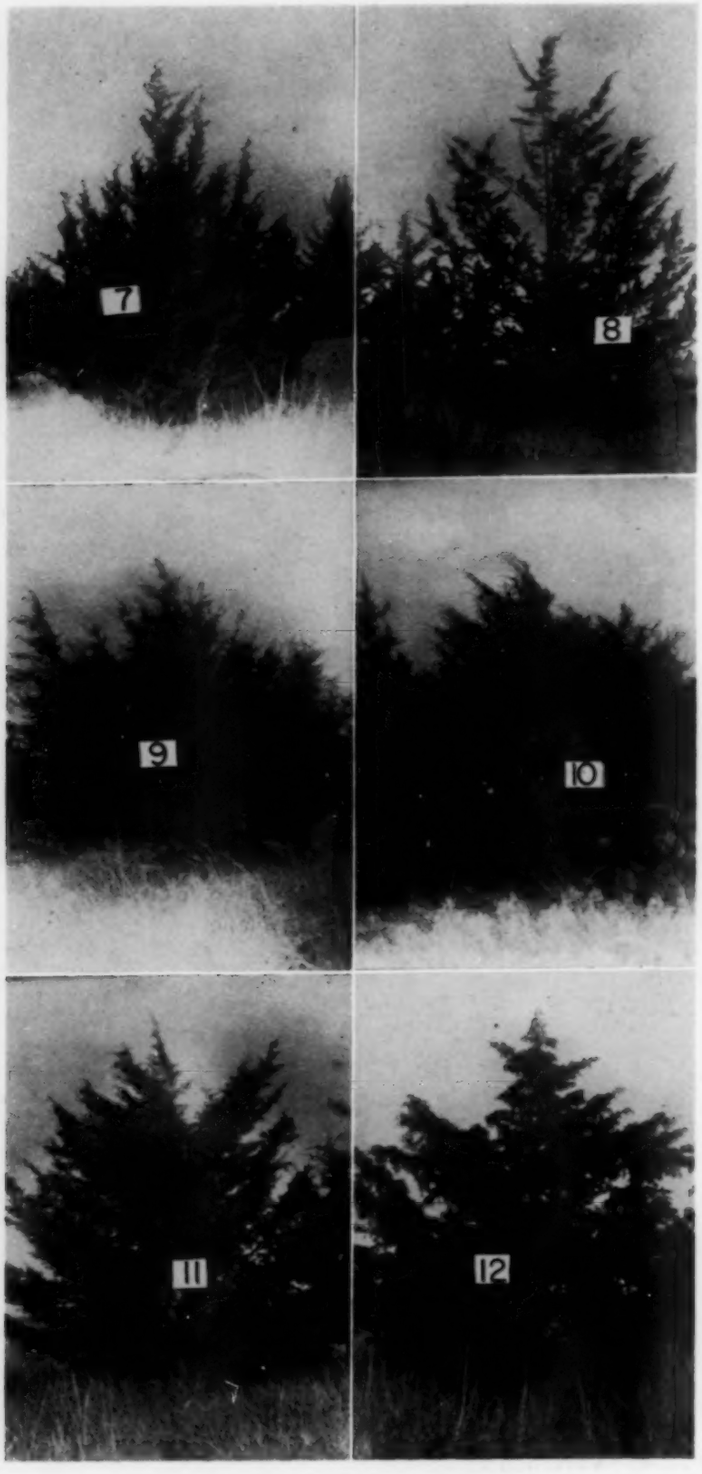

FIG. 5. Variation in habit.

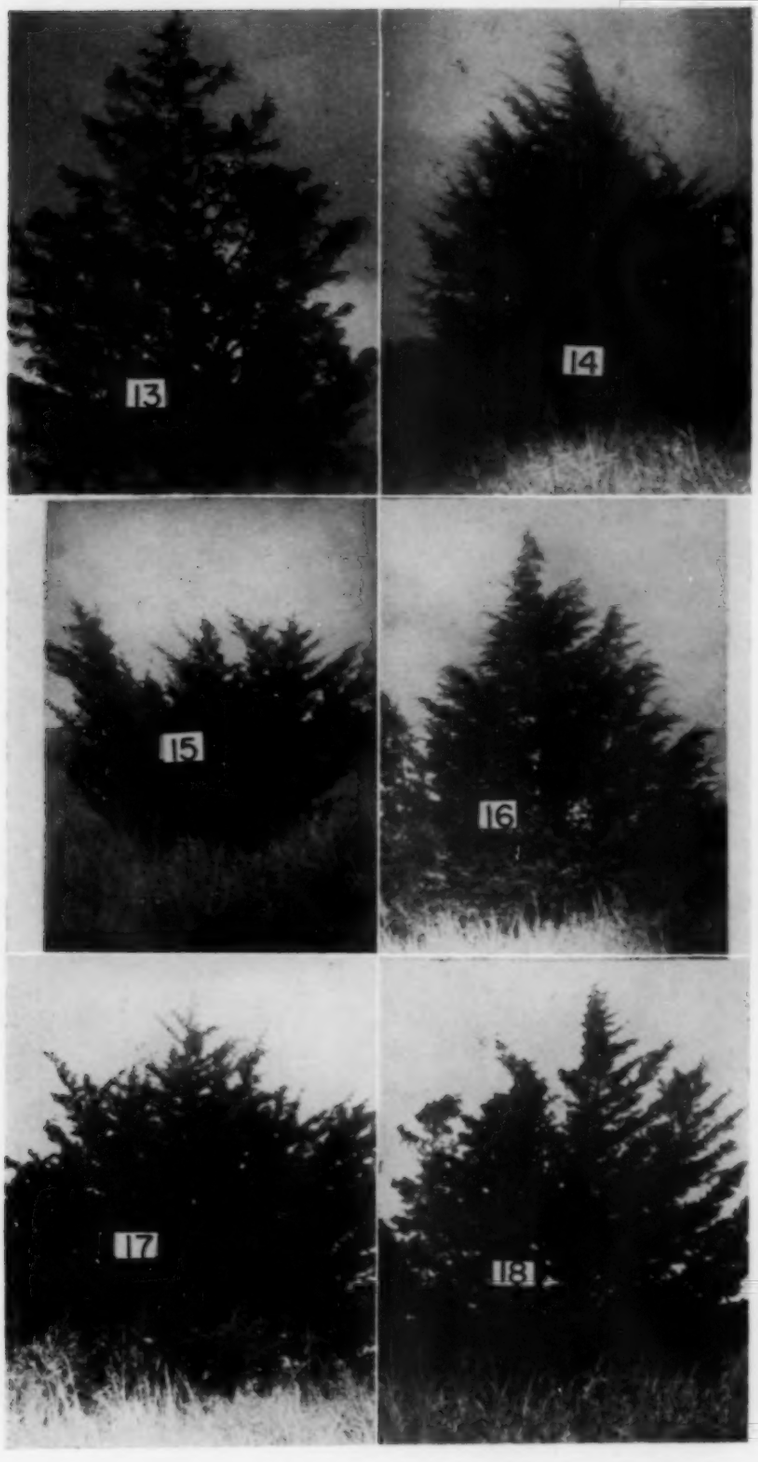

FIG. 6. Variation in habit.

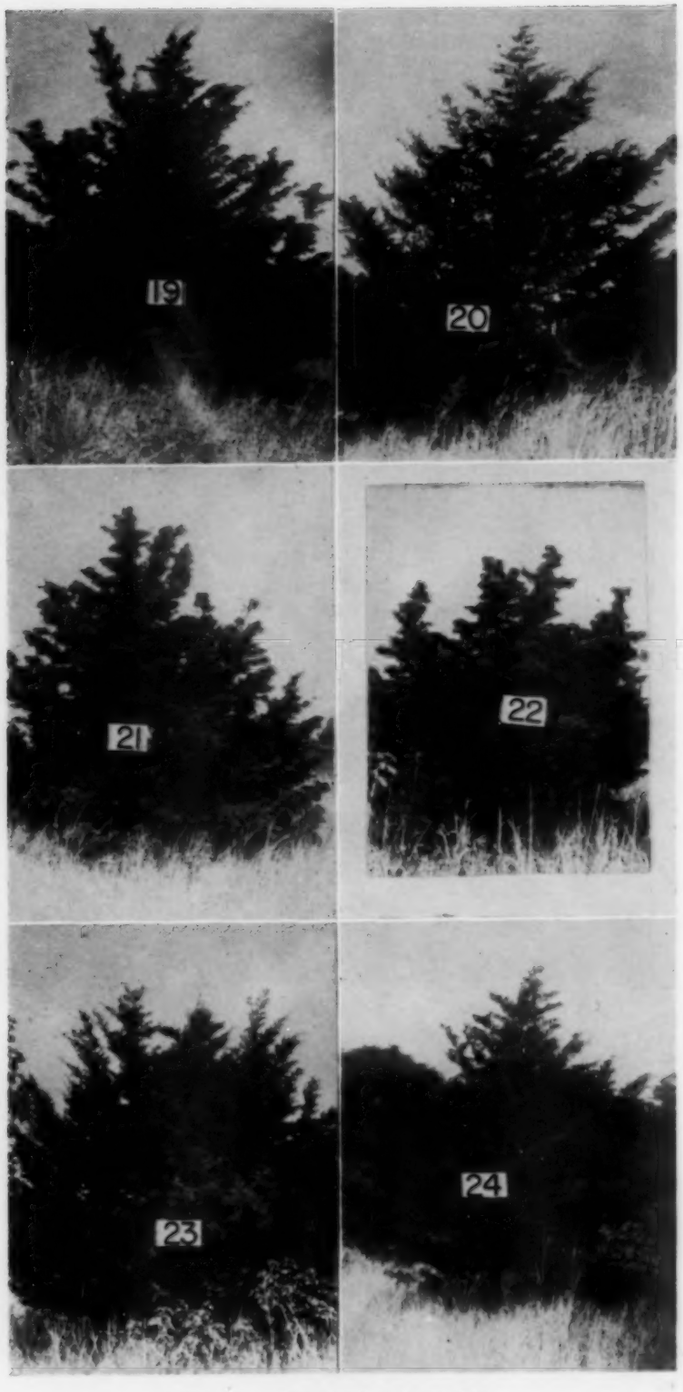

FIG. 7. Variation in habit.

The final check of technique was the repeated scoring of the same population. The population was scored (based on the five characters outlined at bottom page 11) several times in late summer, fall, or winter through a period of three years. In every scoring the resultant grouped data gave nearly the same distribution of the numbered specimens while the overall pattern remained practically identical.

Since in scientific work one is restricted to the study of a partial spectrum of reality, one is destined to receive in return partial reflections of that reality. It is clear that the size of the "universe" studied must be restricted for practical considera-

tions. What is the smallest portion of a population that will demonstrate not only the most often repeated variations but also the extremes? By trial and error methods it was determined that twenty-five specimens safely described the population parameters. The individuals within the population were classed according to age. Three classes were set up: old junipers, those over 47 years; mature junipers (rarely having any juvenile foliage), those between 17 and 47 years; and youthful junipers (commonly having some juvenile foliage), those between 1 and 16 years. Within each species age was correlated fairly well with size at least within a geographic province. These classes were sub-divided into five-year intervals and the morphology of each age class was studied, but the final measurements of characters were made on plants within the mature age class between 25 and 35 years old. This mature class was then sampled by the usual random numbers table technique giving a random sample as to areal distribution for that particular class.

Another method is to sample across the habitat along the route of most obvious environmental differences. In this way the first twenty-five specimens of the mature class would be sampled. This technique is likely to bias the population sample toward the extremes. The most desirable collecting methods are those which result in a sample most closely typifying the frequencies of all the variations in a population.

Character Analysis. In the Platt National Park population more than one hundred plants approximately the same age (30 ±5 years) were numbered and twenty-five of these selected by a random tables technique. These twenty-five trees were photographed and each photograph was standardized to show the growth forms of the plants to scale. Then from each numbered tree was collected and correspondingly numbered the following: (1) a typical secondary shoot approximately 20 inches long, (2) a sample of whip leaves, (3) a sample of spur leaves, (4) a sample of mature berry-cones or staminate cones. The secondary shoots were sampled and diagrammed to scale in figure 3. Secondary shoots of *J. virginiana* (Eastern race) from the Interior Low Plateaus are shown in two columns at the left. Equivalent shoots of *J. Ashei* from the Edwards Plateau are shown in two columns on the right. Secondary shoots from individuals of the hybrid swarm are shown in the four central columns arranged in order of their affinity to one or the other species. Each diagram represents a secondary shoot twenty inches long. On these shoots every lateral branch four inches long or longer was drawn to scale. The following characters are illustrated in this figure: (1) relative length and number of lateral branches per unit of major branch or secondary shoot, (2) angle at which the laterals leave the secondary shoot, (3) length of the terminal whip or long-shoot growth (terminal fine lines of figure 3), (4) length of the lateral whip (lateral fine lines of figure 3), (5) amount of terminal and lateral whip which is ternate (acute bars in fine lines in figure 3) or decussate (horizontal bars on fine lines in figure 3). Hundreds of secondary shoot diagrams were made but only thirty-two were illustrated. The diagrams were placed into four groups, typical *J. virginiana* (Eastern race), typical *J. Ashei* (Central Texas), hybrids most resembling the former species, and hybrids most resembling the latter species; these hybrids were all from the one population. The diagrams to be illustrated were selected at random from each group. There are not enough examples in the illustration from which to draw conclusions; however, the trends with respect to these five characters of the secondary shoots are clearly demonstrated.

These secondary shoots were also scored for the following five characters: (1) gland length-width ratio, (2) length of whip leaf, (3) length of terminal whip, (4) length of lateral whip, (5) on the twenty-inch secondary shoot, the per cent of tertiary branches which have the decus-

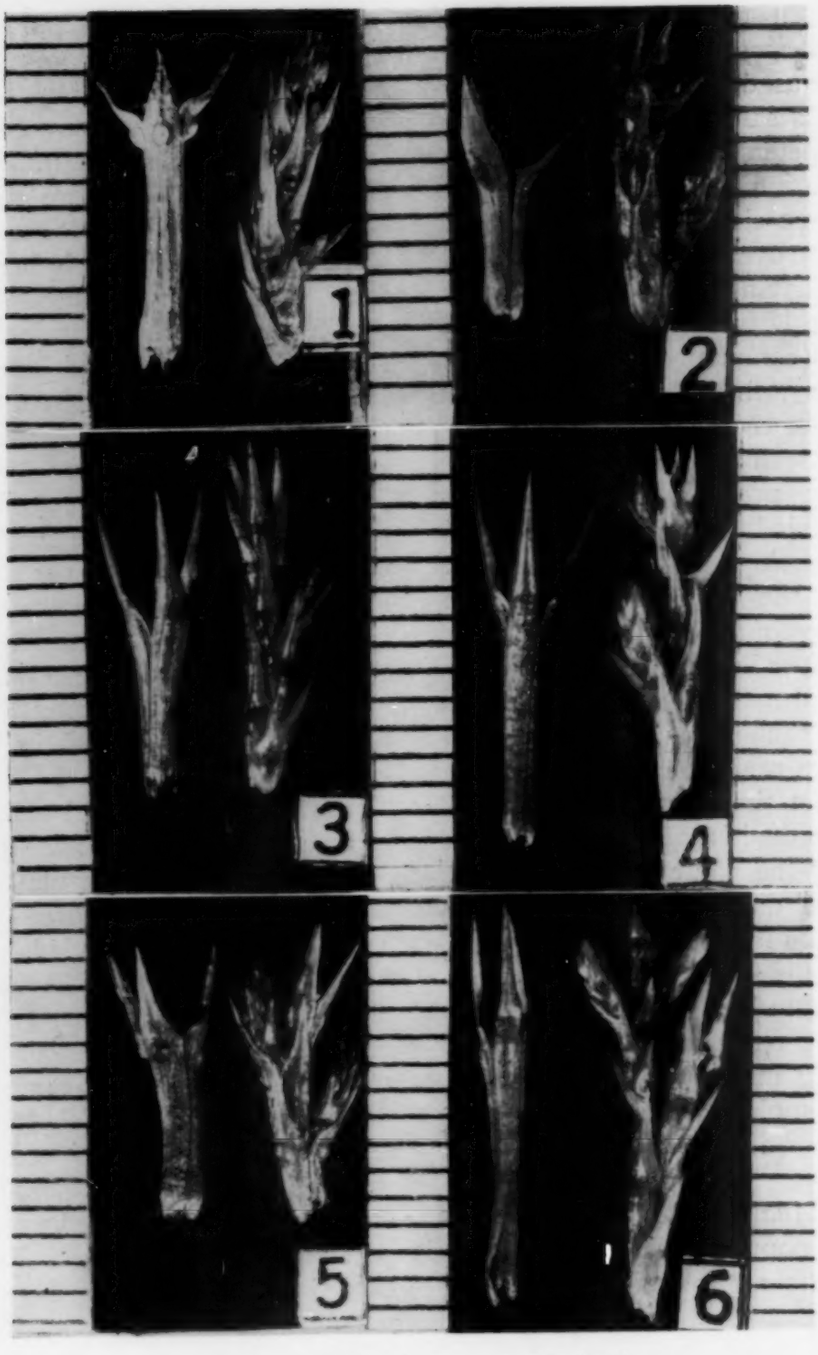

FIG. 8. Variation in leaves and glands.
Scale is in millimeters.

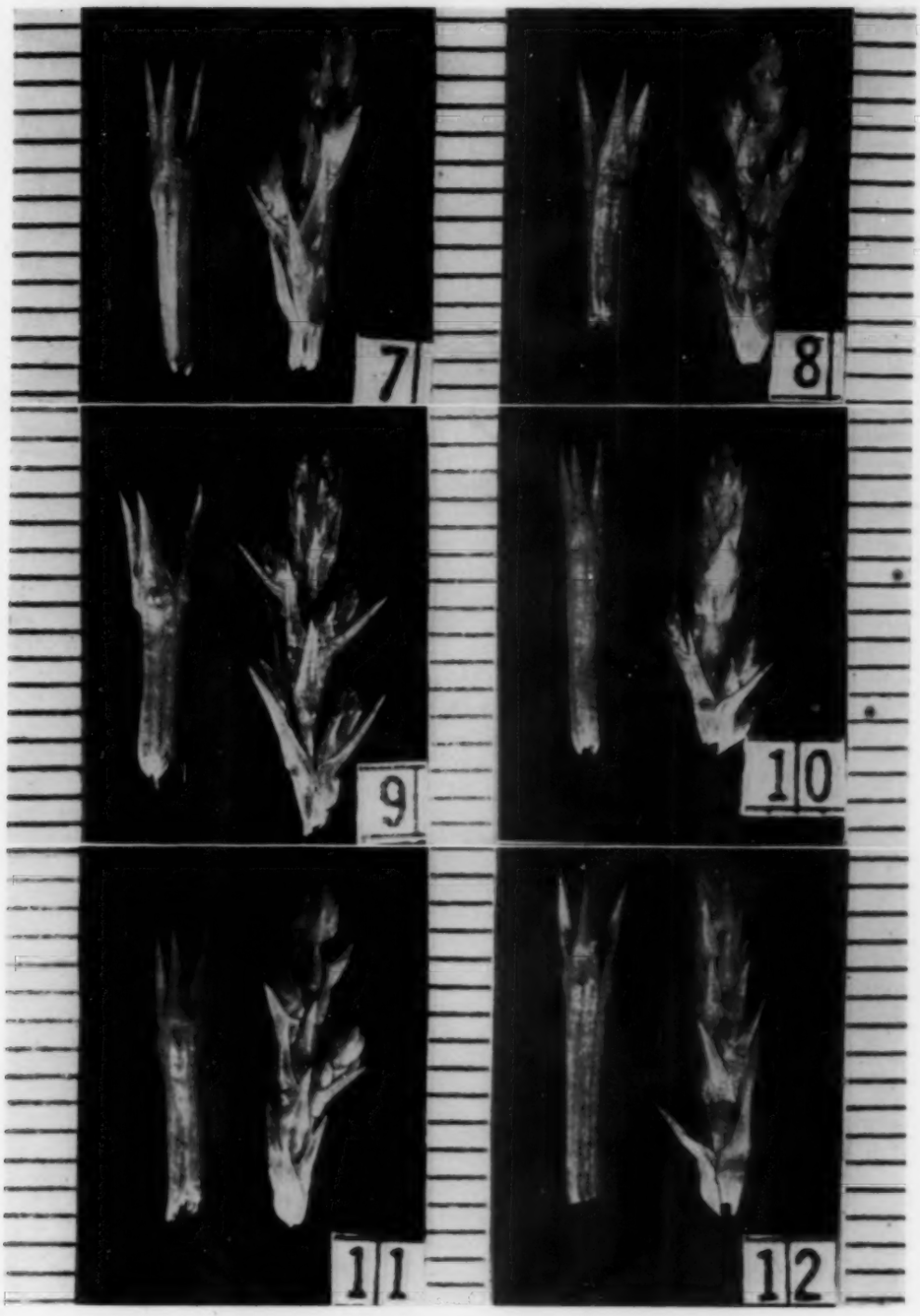

FIG. 9. Variation in leaves and glands.
Scale is in millimeters.

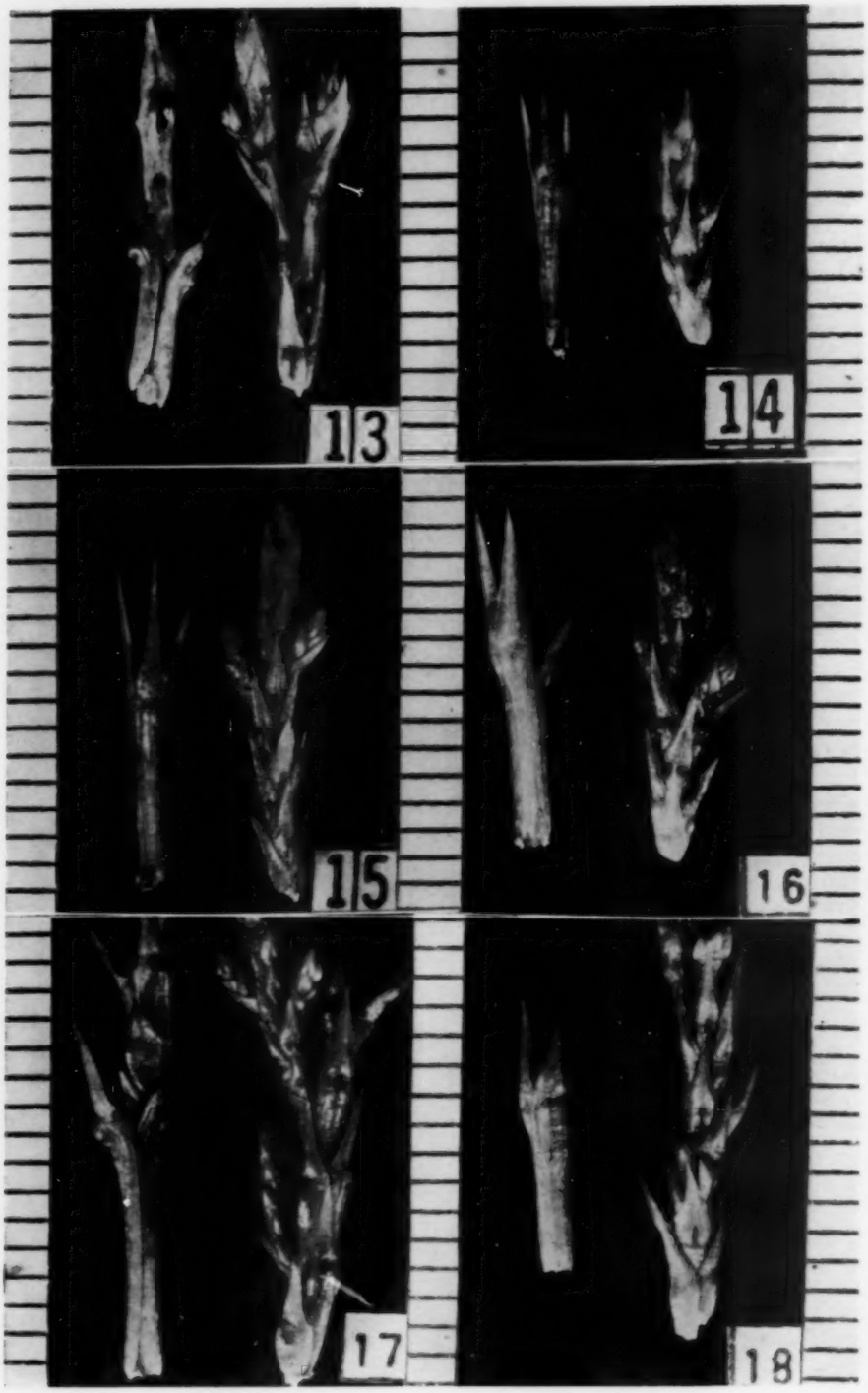

FIG. 10. Variation in leaves and glands.
Scale is in millimeters.

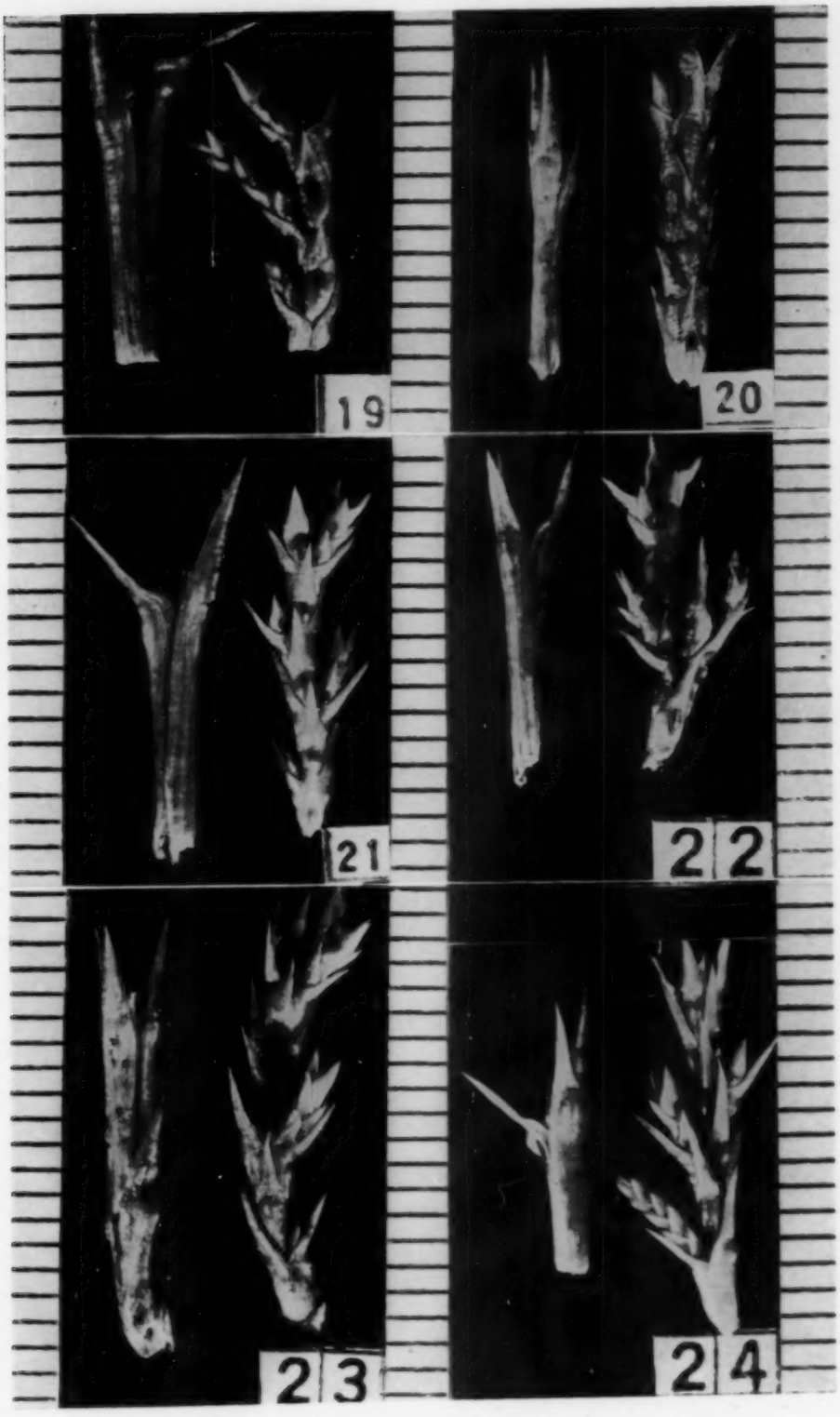

FIG. 11. Variation in leaves and glands.
Scale is in millimeters.

sate leaf arrangement. These characters are described in detail in an earlier paper (Hall, 1952). As explained in the legend of figure 12, the data were grouped into three classes: *Ashei*-like characters, intermediate characters, and *virginiana*-like characters. The grouped data were made into a pictorialized scatter diagram which shows the structure of the Platt hybrid swarm with respect to these five characters (see figure 12). In figure 12 populations of typical *J. Ashei* and typical *J. virginiana* scored for these characters fall within the boundaries so labeled.

The individual plants selected by means of a random numbers table were then numbered from 1 to 24 with permanent field numbers as their secondary shoots were sampled. Standardized photographs were made of each numbered juniper. These habit photographs (figures 4 through 7) clearly show the marked dis-

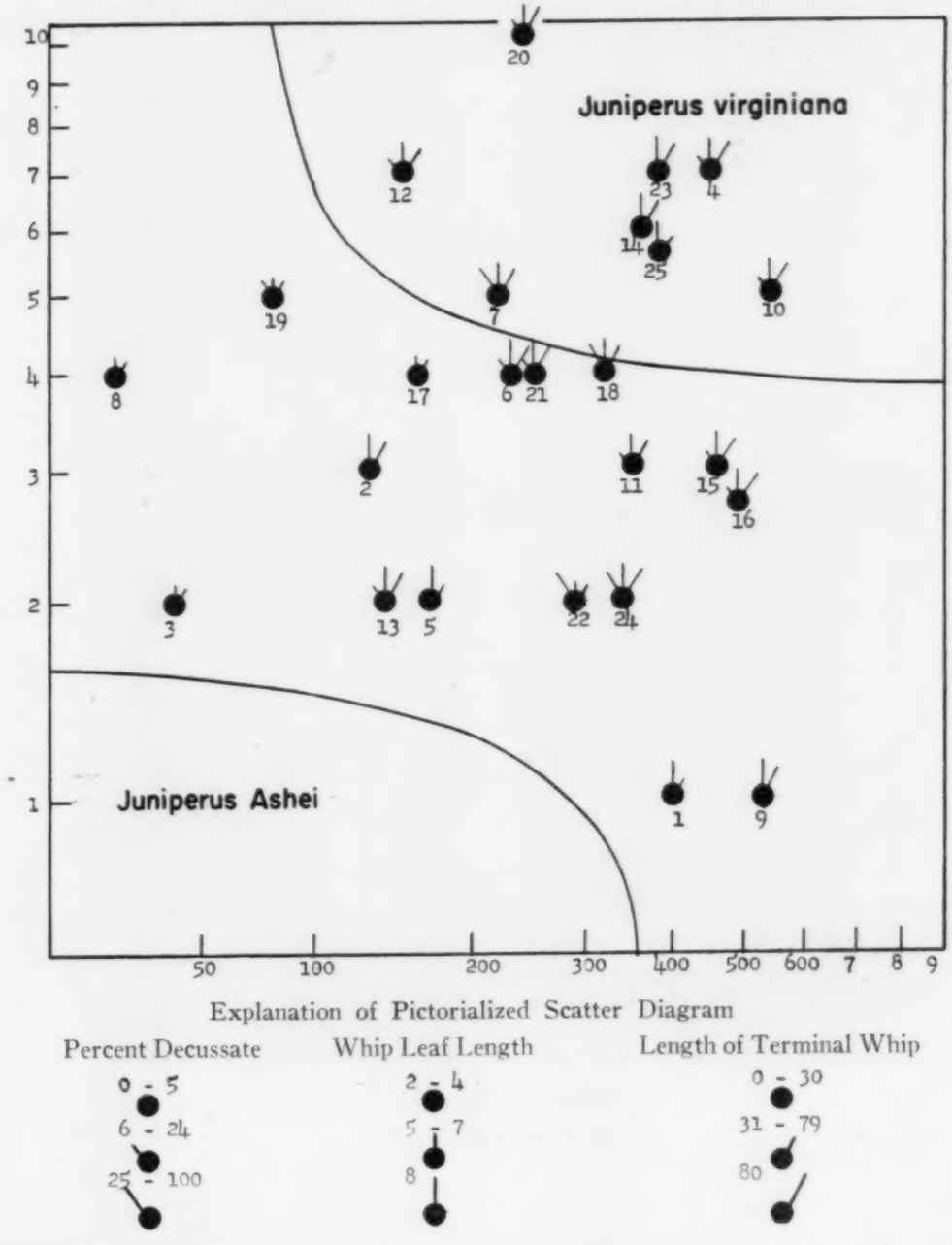

FIG. 12. Scatter diagram showing hybrid swarm between *J. Ashei* and *J. virginiana*.

TABLE 1. *Sequence of specimens using different characters*

Numbers correspond to those of figures 4 through 12

T whip	22	19	13	5	8	1	3	17	2	21	18	11	15	9	14	12	23	16	20	10	7	24	6	4
Gland	9	1	3	22	5	13	24	2	11	15	16	8	17	18	21	6	19	10	7	14	12	23	4	20
Habit	1	9	5	3	2	22	21	15	17	8	13	19	24	6	11	23	14	7	18	12	16	10	4	20
L whip leaf	3	19	22	8	17	1	2	14	12	11	18	5	15	16	21	6	9	13	10	23	4	24	7	20
L lat. whip	8	3	19	2	13	12	17	5	7	6	20	21	22	18	24	11	14	23	1	4	15	16	9	10
Index of all 5 char.	3	5	17	8	1	2	22	13	19	9	21	24	6	11	14	23	18	15	16	12	7	10	20	4

← Most *Ashei*-like specimens

Most *virginiana*-like specimens →

cordance in gross morphology which is so frequently characteristic of hybrid individuals. In these photographs the white plate bearing the number is approximately one foot on its vertical edge. The numbers on these photographs correspond to those on figures 8 through 11 (variation in leaves and glands), figure 12 (pictorialized scatter diagram), and table 1. By comparing the same numbers from figure to figure, one may realize in the hybrids the combinations of characters of the two species.

These numbered specimens are at random and are arranged in order according to their permanent field numbers. To arrange these specimens in order of their affinity to one or the other species, one may use an index of the five characters diagrammed in figure 12. If these illustrations depict a hybrid swarm, one may not expect the specimens to sort into an identical sequence for any two characters since any particular characteristic would be expressed to different degrees in different individuals; but by increasing the number of characters to make an index, one may finally get the minimum number of characters which results in the same numbered sequence again and again. A rough hybrid index may be constructed by assigning values to the grouped data of figure 12. The bar values may be assigned as follows: no bar—0, half-bar—1, whole bar—2. The position of the coordinate may be assigned by breaking the whole diagram up into twenty-five sub-grids ranging from value 0 for the lower left (*J. Ashei*) sub-grid to value 8 for the upper right (*J. virginiana*). Typical *J. Ashei* would have values from 0 to 3, no bars (or half-bars) and 0 sub-grid. Typical *J. virginiana* would have values from 9 to 13, 4 to 5 for bars and 5 to 8 for sub-grid. This particular crude index is roughly the mean value for the five characters of each member of the population.

This index may be converted into an index polygon for the purpose of comparing the total range of variation with respect to all the measured characters for the species and the various populations of intermediates. Figure 13 shows smoothed index polygons for populations of *J. Ashei* (A, A^1) from central Texas, *J. virginiana* (V, V^1) from the Interior Low Plateaus, and for the Platt National Park hybrid swarm (H). This "bird's-eye-view" of each population is useful when comparing populations against their habitats. In the Arbuckles there is a definite correlation between the shape and position of the index curve and the general aspect of the habitat. Detailed studies of these habitats have not yet been made, so that it is not possible to say that the degree of intermediacy is the same for the habitat as for the population.

DISCUSSION

The presence of hybrid swarms of *J. Ashei* and *J. virginiana* where these species occur together in sufficient numbers is evidence that there are at most only slight barriers to hybridization between these species. Hybrid swarms may serve as Nature-made progeny tests for the

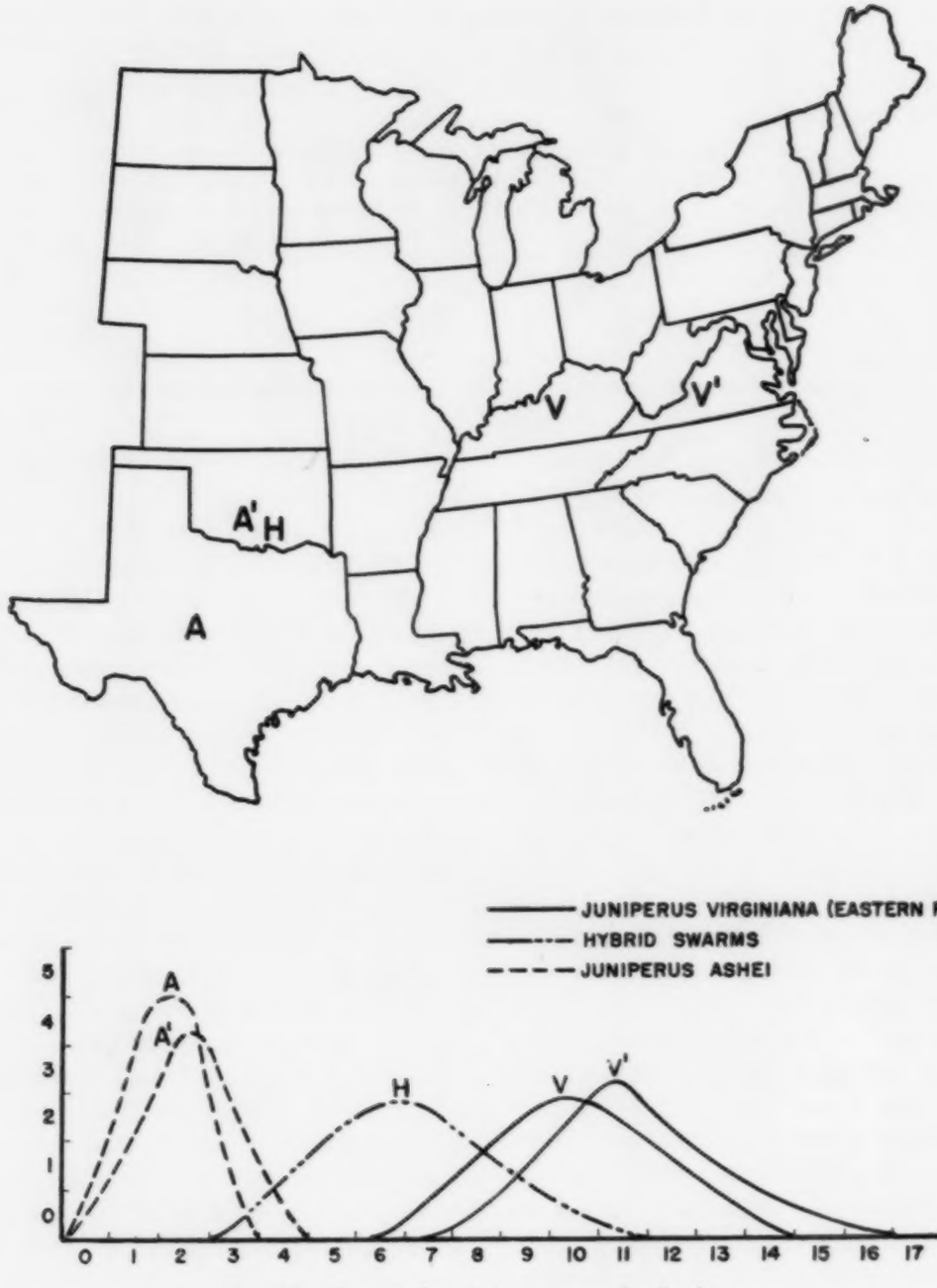

FIG. 13. Population index curves in *Juniperus*.

study of the behavior of specific or subspecific characters when they come together. Careful study of figures 3 through 12 will show the way the characters of the two species behave within a hybrid swarm. Every character illustrated has been influenced through hybridization; even so there is a strong tendency for the characters of the species to stay together. Most of the hybrids with wide angles of branching also have reduced terminal whip with the ternate leaf arrangement, suppressed lateral whip, and very few long lateral branches. These are characters of *J. Ashei*. A few of the hybrids show more extreme character patterns, at least for some characters, than is typical for the species. For example, hybrids resembling *J. Ashei* in most characters often have either very little or no terminal whip on the secondaries; such plants have a very stubby aspect. The scatter diagram (fig-

ure 12) like the hybrid index curve (H curve, figure 13) shows a greater influence of *J. virginiana* over *J. Ashei* in the Platt National Park population. In part, this is the result of differential selection since the Pontotoc conglomerate is quite sandy in the area supporting the hybrid swarm, and hybrids close to *J. Ashei* would likely be under handicap since the species is strongly calciphilous. As a matter of fact, the areas where the hybrid swarms reach their best development are always strongly calcareous, *e.g.*, the bald knobs of south-western Missouri and limestone bluffs of north-western Arkansas. However, the main factor contributing to the slight right skewness of the H curve is probably the differential pollen production and the relative abundance of the two species. *J. Ashei* produces nearly twice as much pollen, plant for plant, as *J. virginiana*. In the vicinity of Platt National Park there are more than twice more specimens of *J. virginiana* than *J. Ashei*. These factors contribute to more favorable numerical relations for Red-cedar and its hybrids in the locality. Wherever these hybrid populations occur, they may become valuable tools for determining similarities and differences in habitats. Where the effects of differences in population structure are known, the results of differential selection may be used for descriptive purposes, and one may determine with some degree of certainty the comparative characteristics of the habitats.

In table 1 the sequences of the numbered specimens in order of their affinity to the species are given for each of five characters and for the index values based on the five characters of figure 12. The specimens numbered 3, 5, 17, 8, 1, 2 are most like typical *J. Ashei* when every character is considered; however, in key characters (gland shape and coarsely denticulate leaf margins) specimens 1, 9, and 5 in that order are most like *J. Ashei*. Reference to table 1 shows that the characters of each species are found in various combinations but not a random. This scattering of the specimens by grouping their numbers according to the same characters does not occur in typical material of either species. However, even in this example of a hybrid swarm the characters of the species tend to associate or stay together in the hybrids. Table 1 shows that habit is the most sensitive indicator of the plant's total character. These specimens, when grouped according to their affinity to the species on the basis of habit, give nearly the same sequence as does the 5-character index. This fact adds strength to the value of gross discordant variation as a clue to inter-specific hybridization.

I believe that hybrid swarms play a very important role in evolution. They represent gene pools, frequently, as in *Juniperus*, of large areal extent from which genes may flow for great distances along many lines of selection. These populations are the key to and the focal point for introgressive hybridization. If these pools of mixed genes are scattered over a good portion of the range of a species, they may serve well as a mechanism for trial and error in the field of gene combinations behaving in somewhat the fashion of a species well differentiated into local contiguous races. Such a species should have good survival value in the face of changing environments. In long lived perennials, particularly woody plants, such hybrid populations often represent the work of numerous years and indicate what may have happened in other situations where introgression has occurred but has not left so great a stamp.

Summary

A hybrid swarm between *J. Ashei* and *J. virginiana* from Platt National Park in the Arbuckle Mountains of southern Oklahoma is illustrated and discussed. Because of the marked morphological and ecological differences between these two species which have similar chromosome numbers, they are good tools with which to demonstrate the behavior of characters in species crosses. Morphological characters of the two species are compared

with those same characters within this hybrid swarm. There are combinations of the characters of both species within the hybrid individuals, but these characters, nevertheless, tend to stay together indicating the probable effect of linkage in hindering gene recombinations of multiple-factor characters.

A hybrid index, roughly the group means of five characters for each individual of the population, was used to construct a frequency polygon for the twenty-five individuals measured. This index offers a crude but effective method for comparing both populations and their habitats, at least, wherever differential selection is the predominate variable affecting population structure.

The value of concordant and discordant variation in a population as a clue to the purity or the hybrid character of its constituents is demonstrated. The probable significance of the hybrid swarm in evolution in allopatric species is discussed briefly.

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INTROGRESSION BETWEEN *TYPHA LATIFOLIA* AND *T. ANGUSTIFOLIA*

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INTRODUCTION

Throughout much of their range in the northern United States and southern Canada, *T. latifolia* and *T. angustifolia* occupy the same regions; many colonies consist of both species, in company with individuals combining characteristics of the two. In many colonies that apparently consist of but one species, some individuals show characteristics of the other species.

The cat-tails of the United States have been referred to four species, *T. latifolia* L., *T. angustifolia* L., *T. glauca* Godr. and *T. domingensis* Pers., by Hotchkiss and Dozier (1949) and their treatment has been followed by Fernald (1950) in the eighth edition of Gray's Manual. The present study would suggest that *T. glauca*, described as somewhat intermediate between *T. latifolia* and *T. angustifolia* by Hotchkiss and Dozier, is not a definite entity, but rather a series of individuals in hybrid swarms. *T. domingensis* ranges south of the area covered in the present study.

COLLECTIONS

From each location shown on figures 4–6, a mass collection was made. Many of these collections were by the authors, travelling in different regions under grants from the Wisconsin Alumni Research Foundation. Collections by others include the following: from Fall Creek, Black River Falls and Morrison Creek, Wisconsin, by D. F. Grether; from locations in Michigan, Gary, Indiana, Sheboygan, Theresa, Wisconsin and Independence, Iowa, by P. J. Salamun, also during travel made possible by the Wisconsin Alumni Research Foundation. The specimens shown in figures 8a and 8b are single individuals in the locations named and are specimens from the Gray Herbarium and the New England Botanical Club.

From each clone one flowering spike and a leaf from the same stem were collected and wired together. Most of the spikes were subsequently dipped in a solution of cellulose acetate to prevent disintegration; DDT was added to the solution to discourage insects. For detailed study, flowers and fruits were washed in acetone to remove the cellulose acetate.

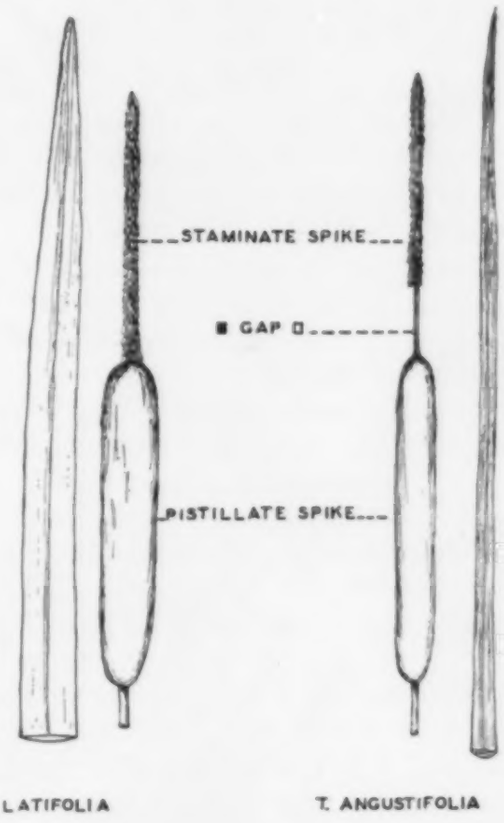

FIG. 1. Spikes and leaf tips, times about 1/3. Solid squares designate characters of *T. latifolia* and open squares characters of *T. angustifolia*, as used in figures 4–8.

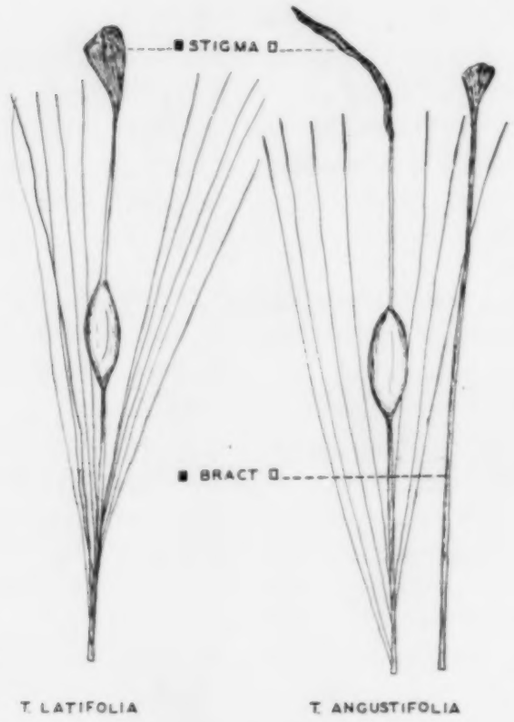

FIG. 2. Pistillate flowers, times about 6.

QUALITATIVE CHARACTERS USED ON THE MAPS

Six characters can quite definitely be determined one way or the other as either a *latifolia* character or an *angustifolia* character. On each grid on figures 4–6, a vertical column represents a character and a horizontal row represents an individual. The number of horizontal rows therefore varies with the number of individuals in each collection. *T. latifolia* characteristics are shown by black squares and *T. angustifolia* characteristics are shown by open squares. For example, all individuals from clones near Rice Lake, Wisconsin (fig. 6), are pure *T. latifolia*; all individuals from Valhalla, New York, (fig. 4) are pure *T. angustifolia*; and at Palatine Bridge, New York, are individuals with both *latifolia* and *angustifolia* characteristics. A square with hatched lines shows that for the specimen indicated the characteristic is intermediate, or also that characteristics of both species occur on the same individual. An example of this is seen at Cos Cob, Connecticut, where both filiform and flattened stigmas are seen on the same individual.

The data presented in summary in figure 7 are based on all the mass collections combined. Here are represented all possible combinations of the same 6 characters used in figures 4–6: the first line is pure *T. angustifolia,* with 86 individuals represented in the mass collections; the second line has the staminate and pistillate portions of the spike contiguous as in *T. latifolia* but has the other 5 characters as in *T. angustifolia,* and is represented by 3 individuals, and so on. Figure 7 corroborates the impression gained from the grids on figures 4–6, that the vast majority of individuals are either pure *T. angustifolia* or *T. latifolia,* and individuals with 5 characters of one species or the other are next in abundance. There are, then, effective forces, external or internal or both, tending to keep the two species separate.

Column 1: Gap between pistillate and staminate portions of spike

This characteristic is shown in Figure 1. On the grids in figures 4–8, this characteristic is represented by the first verti-

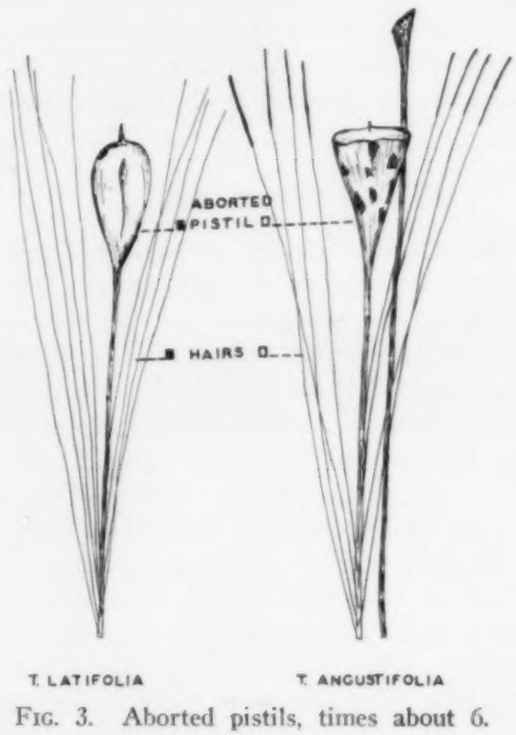

FIG. 3. Aborted pistils, times about 6.

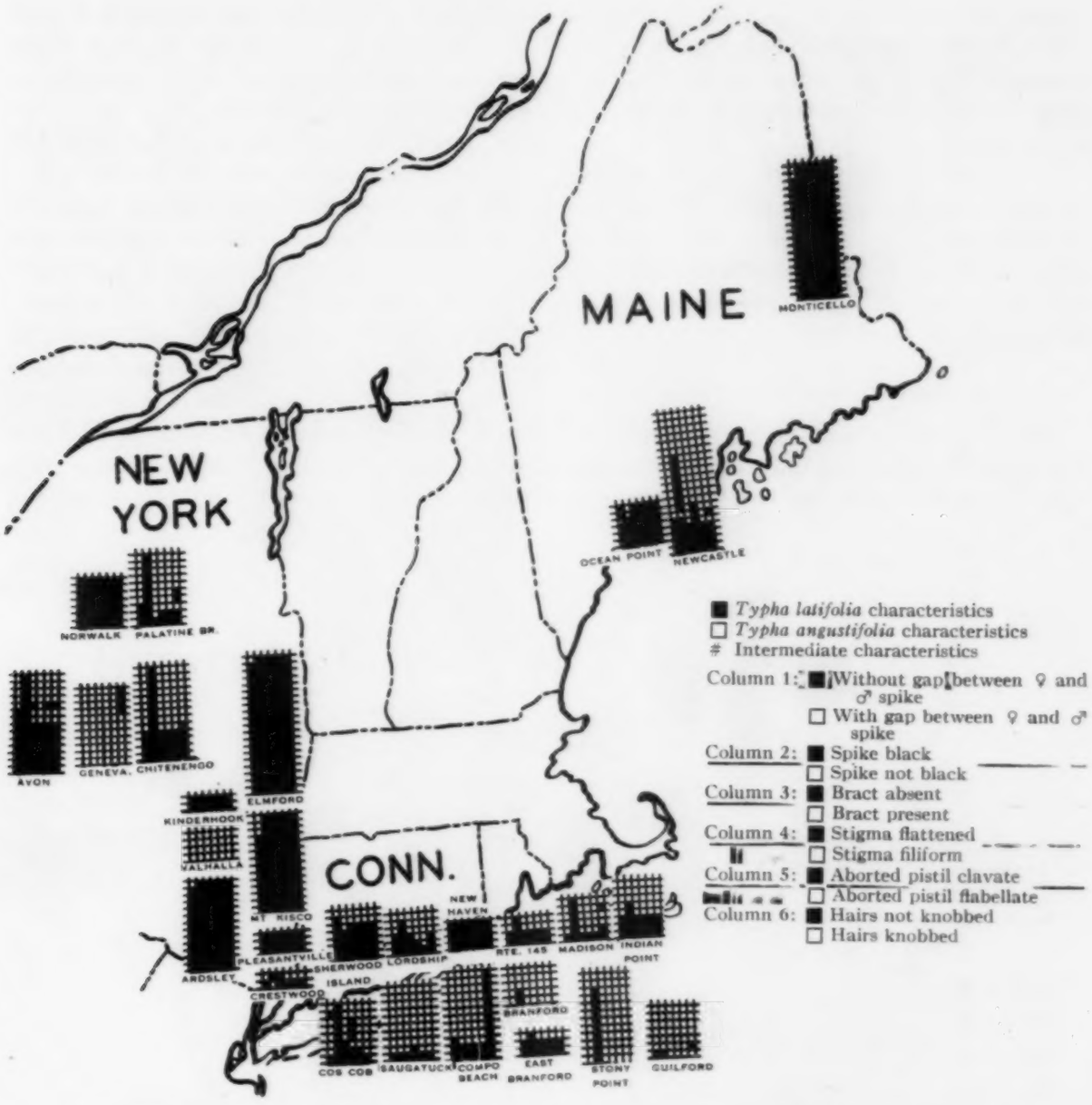

FIG. 4. Colonies of *Typha* in New England and New York. Each horizontal line of squares represents an individual; each vertical column represents a character, as shown in figures 1–3.

cal column. The absence of the gap between the pistillate and staminate portions of the spike in *T. latifolia* is indicated by a black square in the first column on each grid. The gap between the two portions in *T. angustifolia* is indicated by an open square in the first column in each grid.

Of the 194 individuals showing 4 or more *T. angustifolia* characters, 183 (94%) have the gap in the spike characteristic of that species. Of the 623 individuals showing 4 or more *T. latifolia* characters, 573 (92%) have the continuous spike characteristic of that species. (Statements derived from data on figure 7.)

It is notable, however, that in several regions where no *T. angustifolia* is known, an occasional individual of *T. latifolia* shows a gap in the spike (Monticello, Maine; St. Ignace and Indian Lake, Michigan; Sarona, Wisconsin), as well as in regions where the two species coexist (eastern Wisconsin). This suggests a

slight tendency for *T. latifolia* to have a discontinuous spike, independent of introgression from the other species. Such individuals have been named *T. latifolia* f. *ambigua*.

Since all of the material of *T. angustifolia* is from regions where *T. latifolia* is also known, it is difficult to determine how much of *T. angustifolia* would have a continuous spike in absence of any introgression.

Column 2: Color of spike

In *T. latifolia* the pistillate portion of the spike is commonly mottled with black; this is represented by black squares in column 2 of each grid in figures 4–8. In *T. angustifolia* the color is clear light brown, represented by open squares in column 2 of each grid.

Of the 623 individuals with 4 or more *latifolia* characters, only 45 (about 7%) lack the black mottling, and of these 45 individuals, some 32 have the light brown spike without other *angustifolia* characters. On the other hand, of the 194 plants with 4 or more *angustifolia* characters, 89 individuals (46%) have the black-mottled spikes of *T. latifolia*, and the 76 plants with mottled spikes combined with 5 *angustifolia* characters nearly equals the number of individuals (86) of pure *angus-*

FIG. 5. Colonies of *Typha* in Michigan, Ontario, Indiana, and Iowa.

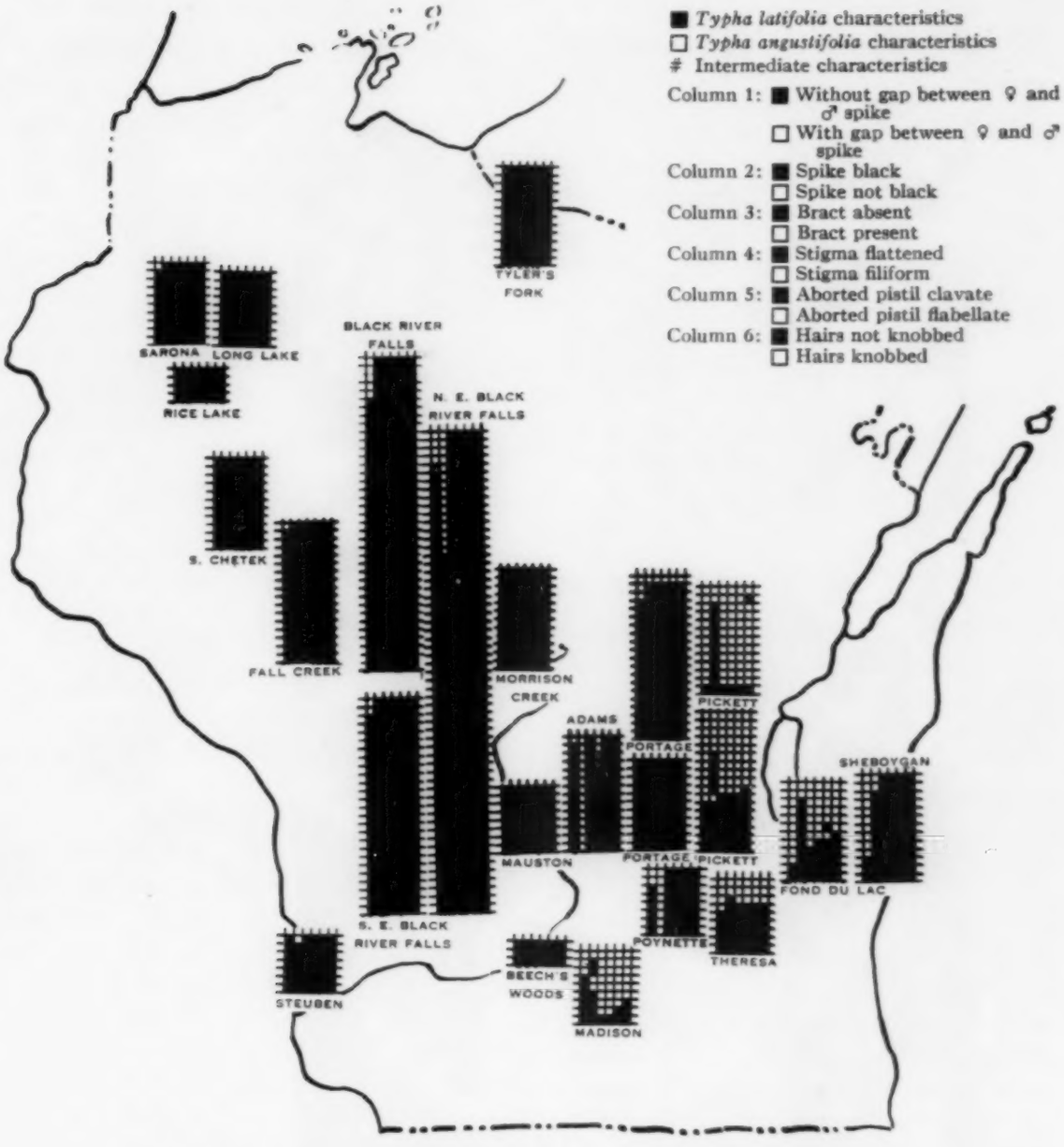

FIG. 6. Colonies of *Typha* in Wisconsin.

tifolia. This may be only a reflection of the fact that throughout much of its range *T. latifolia* is beyond regions where *T. angustifolia* grows, whereas *T. angustifolia*, in its entire North American range, is not far from the influence of *T. latifolia*.

At several localities in eastern New York, Connecticut, Maine and Wisconsin, colonies may include a majority of individuals that would appear to be pure *T. angustifolia* were it not for the black-mottled spikes; note, for example, the long black second column of Stony Point, Connecticut. The reciprocal arrangement occurs at several points in central Wisconsin where many plants appear to be pure *T. latifolia* except for the unmottled spikes. These are probably not merely cases of many individuals being taken from one clone, for differences appear in size and shape of spikes.

Column 3: Pistillate bract

In Graebner's treatment of *Typha* in the Pflanzenreich (1900) *T. angustifolia* is

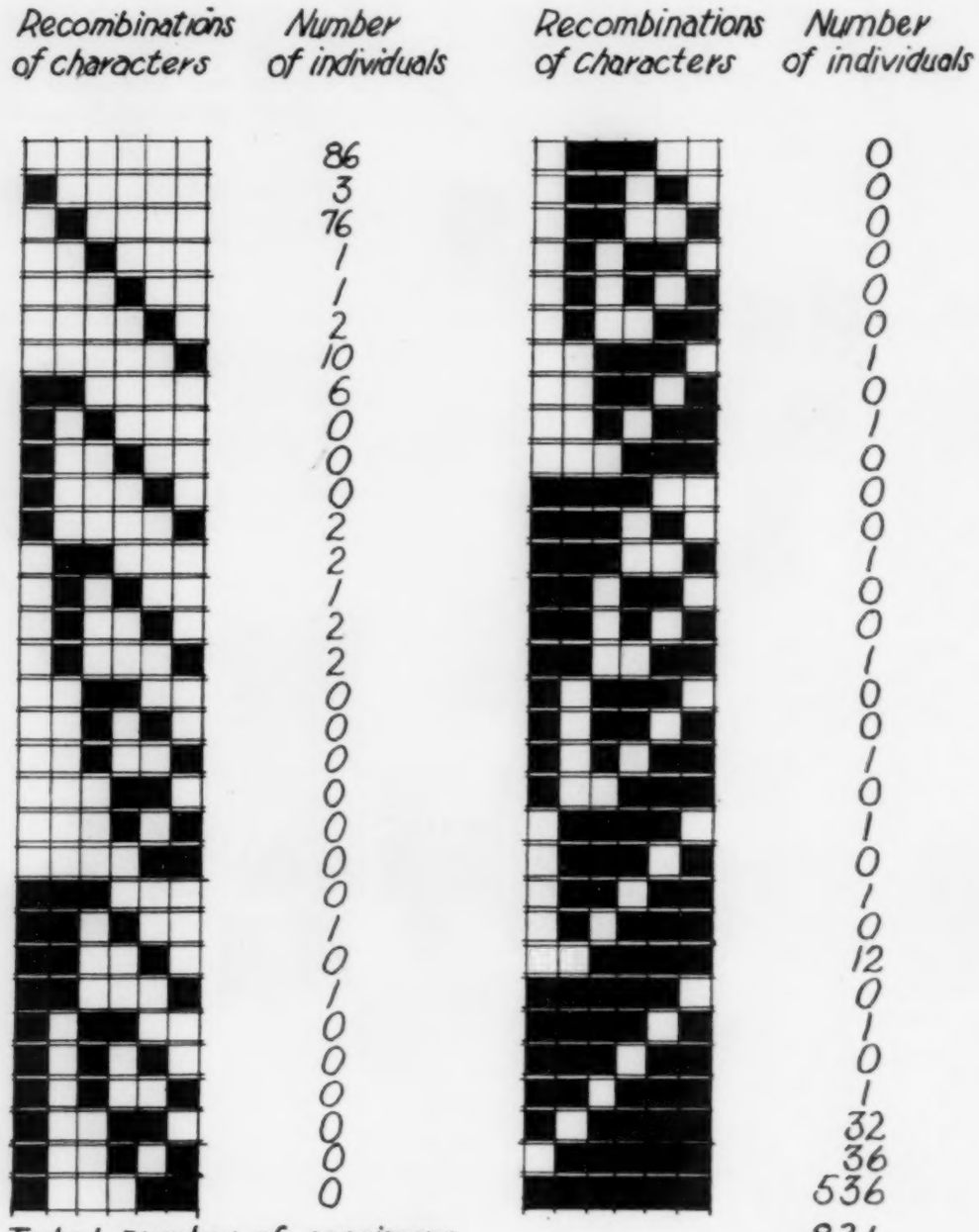

FIG. 7. Each horizontal line shows a possible combination of characters of *T. angustifolia* (open squares) and of *T. latifolia* (solid squares), as in figures 4–6. The 821 individuals were from the mass collections shown in figures 4–7, plus a few more from the same regions.

put in the section Bracteolatae, characterized by the possession of a hairlike bract with spatulate tip, at the base of the pistillate flower, while *T. latifolia,* in Section Ebracteolatae, lacks such a bract. The bract is illustrated in figures 2 and 3.

If a "good taxonomic character" is one that correlates well with other characters of the same species, then this is a "good" character. Of the 194 individuals with 4 or more *angustifolia* characters only 3 lack the bract, and of the 623 individuals with 4 or more *latifolia* characters only 2 have the bract. (Data in figure 7: An open square in column 3 represents presence of the bract as in *T. angustifolia*; a black square represents lack of bract as in *T. latifolia.*)

Column 4: Form of stigma

A filiform stigma is typical of *T. angustifolia* and a flattened stigma is typical of *T. latifolia* (fig. 2). Of the 196 specimens with pistillate bract, 91% have a filiform stigma. Of the 626 specimens in which the bract is absent, 99% have a flattened stigma. Or, in other words, of the 821 individuals recorded in figure 7, for only 11 are columns 3 and 4 different.

A few individuals have both filiform and flattened stigmas. Three specimens were from Cos Cob, one from Madison, Connecticut, two from Adams, Wisconsin, and one from Newcastle, Maine. Other individuals, otherwise predominantly of the *angustifolia* type, have filiform stigmas or stigmas of an intermediate type.

Column 5: Shape of aborted pistil

The aborted pistils, which are often abundant among the mature fruits, have been described by Celakovsky (1885); the present authors have also found their shape to be diagnostic (fig. 3). In *T. latifolia* the aborted pistil is club-shaped or pear-shaped, rounded at apex with an abrupt point; the color is light buff, and a cross-section shows a sharply defined central space with two locules. In *T. angustifolia* the aborted pistil is flattened and wider at the tip; the color is darker buff with reddish-brown spots, and the locule is much reduced.

Of the 623 individuals with 4 or more *latifolia* characters, only two have the aborted pistil usually characteristic of *T. angustifolia*; of the 194 individuals with 4 or more *angustifolia* characters, four have the aborted pistil of *T. latifolia*.

An individual from Madison, Connecticut, has both aborted pistils of the *angustifolia* type and those of an intermediate form. An aborted pistil of an intermediate form is described by Hotchkiss and Dozier (1949) as typical of *T. glauca*.

Column 6: Pistillate hairs

From the base of each pistillate flower comes a copious tuft of delicate white hairs; it is these hairs that are primarily responsible for the feathery nature of cattail down. In *T. angustifolia* each hair is terminated by a minute dark enlargement at the tip (figs. 2 and 3) which is lacking in *T. latifolia*.

The correlation of this character with those of columns 4 and 5 is nearly perfect A notable exception is at Compo Beach, Connecticut, where a majority of the individuals, while having all the other characters of *T. latifolia*, have the knobbed hairs of *T. angustifolia* (cf. behavior of spike color, column 2).

An intermediate condition is found in some individuals along the coast of Connecticut.

CHARACTERS NOT USED ON THE MAPS

Several sets of characters, among them some fundamental ones separating the two species, have not been used on the maps or the graph. In most cases this has been either because they were of a quantitative nature and so not adaptable to the graphic methods used, or because they could not be observed on all individuals.

Proportions of pistillate portion of spike

Although the two species are usually distinguished at a glance by the size and shape of the pistillate portion of the spike, there is much overlap and variation of this character. Authors have listed a broad (2.5 cm. max.) and long (15 cm. max.) pistillate spike for *T. latifolia* and a more slender (1.0–1.7 cm.) and shorter (8–13 cm.) pistillate spike for *T. angustifolia*, but there are many variations. One of these variations, *T. angustifolia* var. *elongata*, has been described by K. M. Wiegand as occurring around Canoga and Cayuga Marshes, the east end of Lake Ontario and about Oneida Lake (Wiegand, 1924). It is treated as *T. glauca* by Hotchkiss and Dozier (1947). It has the main characteristics of *T. angustifolia* except that the pistillate spike measures 15–30 cm. long, and 2.0–2.3 cm. thick. It probably represents *T. angustifolia* with some introgression from *T. latifolia*.

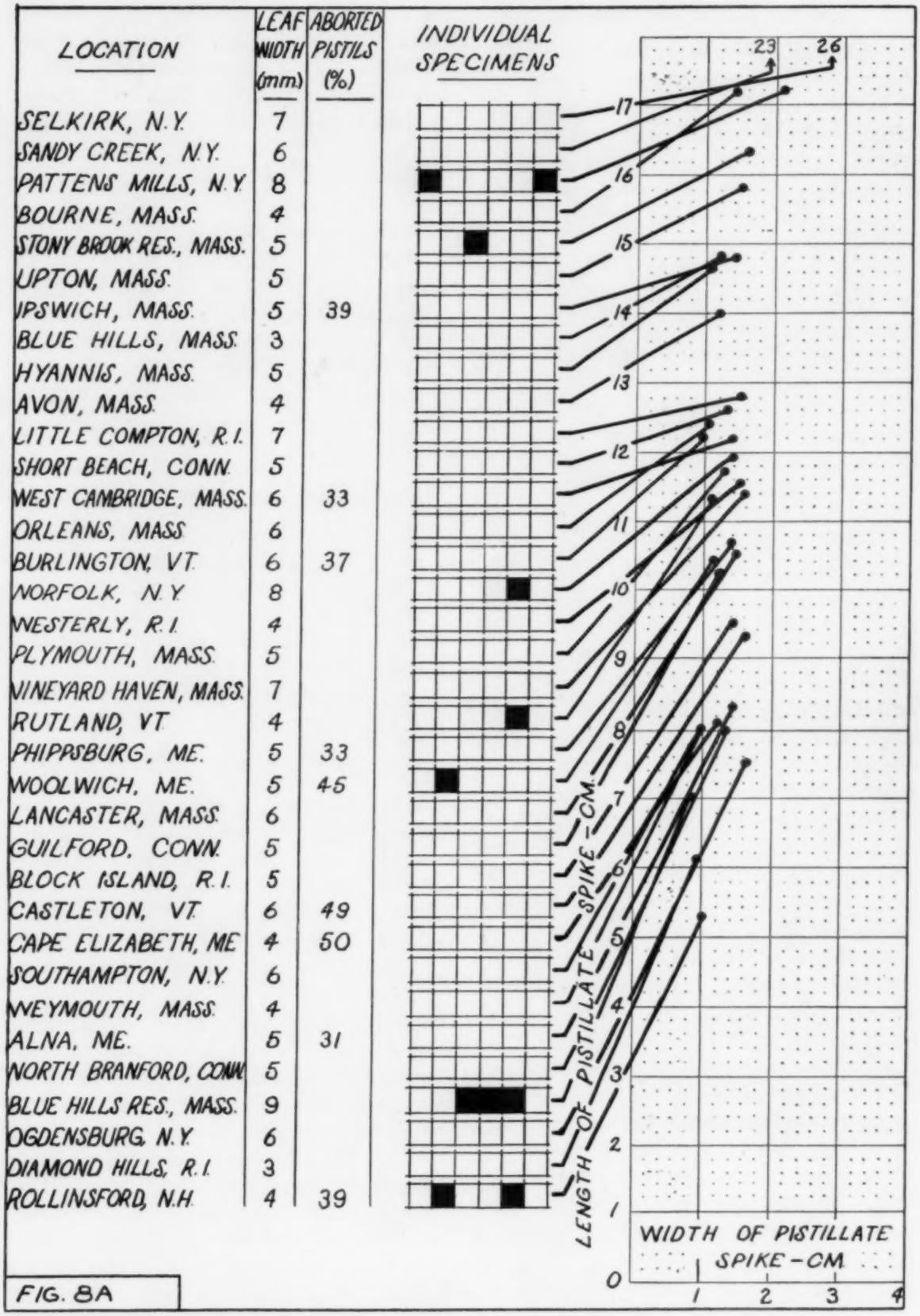

FIG. 8. Measurement of pistillate spikes of 68 individuals of *Typha* in the Gray Herbarium and Herbarium of the New England Botanical Club. The location of the dot on the grid to the right shows length and thickness; the grid is actual size and the appearance of each spike

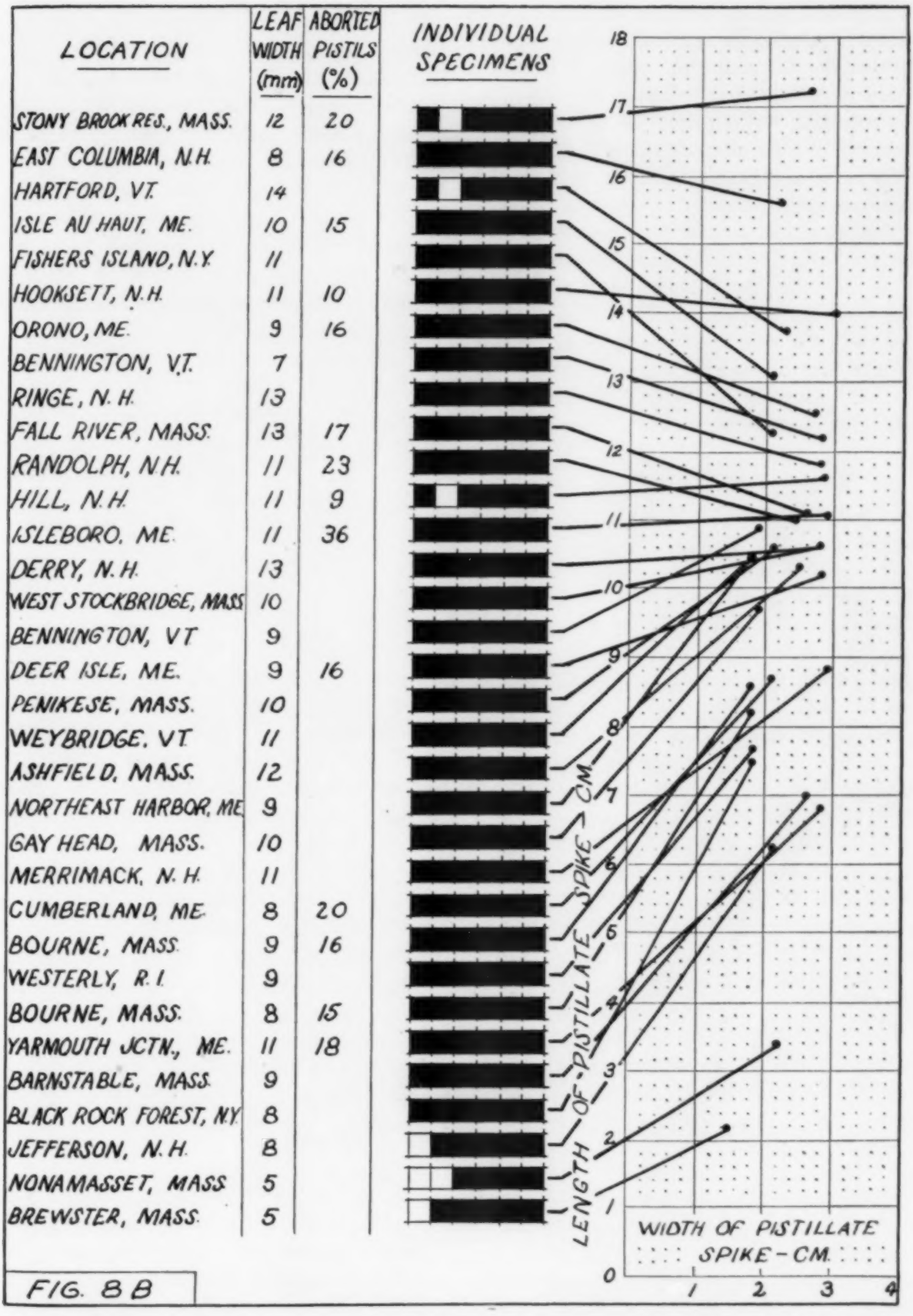
LOCATION
LEAF WIDTH (mm)
ABORTED PISTILS (%)
INDIVIDUAL SPECIMENS
STONY BROOK RES., MASS. 12 20
EAST COLUMBIA, N.H. 8 16
HARTFORD, VT. 14
ISLE AU HAUT, ME. 10 15
FISHERS ISLAND, N.Y. 11
HOOKSETT, N.H. 11 10
ORONO, ME. 9 16
BENNINGTON, VT. 7
RINGE, N. H. 13
FALL RIVER, MASS. 13 17
RANDOLPH, N.H. 11 23
HILL, N.H. 11 9
ISLEBORO, ME. 11 36
DERRY, N.H. 13
WEST STOCKBRIDGE, MASS 10
BENNINGTON, VT 9
DEER ISLE, ME. 9 16
PENIKESE, MASS. 10
WEYBRIDGE, VT 11
ASHFIELD, MASS. 12
NORTHEAST HARBOR, ME 9
GAY HEAD, MASS. 10
MERRIMACK, N. H. 11
CUMBERLAND, ME. 8 20
BOURNE, MASS. 9 16
WESTERLY, R. I. 9
BOURNE, MASS. 8 15
YARMOUTH JCTN., ME. 11 18
BARNSTABLE, MASS. 9
BLACK ROCK FOREST, NY 8
JEFFERSON, N.H. 8
NONAMASSET, MASS 5
BREWSTER, MASS. 5
LENGTH OF PISTILLATE SPIKE CM.
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
WIDTH OF PISTILLATE SPIKE - CM.
0 1 2 3 4

FIG. 8B

can be visualized. In the column under the heading "Individual Species," the six characters of each individual are indicated, in the same manner as in figures 4–7.

In this study on the mass collections the evidence would seem to show that the interspecific difference between the proportions of the pistillate spikes is less than the intraspecific variation in patterns of proportions. Obviously, to study introgression as evidenced by this character would require large amounts of material and intense statistical research. Figures 8a and 8b, showing one individual from each location, link the six characteristics shown in the grid (to the left) with the length and width of the pistillate spike (to the right). There may be an indication that the longest and shortest spikes are on individuals showing mixed characters.

Pollen grains

Of the 215 individuals with pollen, a great majority showed correlation with other characters: for example, 159 individuals have the flattened stigma of *T. latifolia* and pollen grains in 4's, while 20 have the filiform stigmas of *T. angustifolia* and pollen grains single. Lack of strict correlation is shown by the six following recombinations of characters: (1) filiform stigmas of *T. angustifolia* and pollen grains in 4's as in *T. latifolia*—3 individuals; (2) flattened stigmas of *T. latifolia* and pollen grains single as in *T. angustifolia*—5 individuals; (3) flattened stigmas and pollen grains both in 4's and singly—17 individuals; (4) filiform stigmas and pollen grains both in 4's and borne singly—6 individuals; (5) stigmas both filiform and flattened and pollen grains in 4's—3 individuals; (6) stigmas both filiform and flattened and pollen grains borne singly—2 individuals.

Compound pedicels

The compound pedicel of the pistillate spike is long, hairlike and jointed in *T. latifolia* and varies in size only with the proportions of the spike. In *T. angustifolia*, these pedicels are short and stubby and are more widely spaced on the spike; they also seem to vary in size only with the proportion of the spike.

Width and cross-section of leaf

In Gray's New Manual (1950) the leaves of *T. latifolia* are described as being 6–23 mm. broad, while those of *T. angustifolia* are 6–15 mm. broad. In Fassett's Manual of Aquatic Plants (1940) the width of *T. angustifolia* leaves is listed as 3–7 mm. In measurements taken of the mass collections, the leaf of *T. angustifolia* ranges from 3–12 mm. in width, while leaf width in *T. latifolia* is 7–20 mm. In the individuals listed in figures 8a and 8b, those with a majority of *angustifolia* characters have leaves from 3–8 mm. wide, and those with a majority of *latifolia* characters have leaves from 7–14 mm. wide. So although *T. angustifolia* tends to have a narrow leaf and *T. latifolia* tends to have a broad leaf, overlapping invalidates the use of this characteristic in positive separation of two species.

The leaf profile (fig. 1) varies from flat in pure *T. latifolia* to definitely rounded in pure *T. angustifolia*. Some plants found near Terry Andrae State Park, Sheboygan, Wisconsin, seem to be pure *T. latifolia* except for the definitely convex lower leaf surface. Although the variation may be great in specimens from one locality, it generally follows that if there are characteristics of one species predominant in a specimen, the leaf profile tends to be characteristic of that species.

It appears, then, that the characters of the leaves behave much as do the qualitative characters; while of specific nature, they tend to move from one species to the other in regions of coexistence and introgression.

Leaf sheath

The study of the characteristic leaf sheath is omitted in this study since that part of the plant was not collected. As described by Hotchkiss and Dozier it would seem to be a good distinguishing characteristic.

Pith

The color of the pith, as described by Hotchkiss and Dozier, is white in *T. latifolia, T. angustifolia* and *T. domingensis* and buff in *T. glauca.* In a study of colonies in the mass collections, slight variation was observed.

Kinds of Colonies

There are various kinds of colonies ranging from pure or nearly pure *T. latifolia,* like many colonies in Michigan, and pure, or nearly pure *T. angustifolia* at Valhalla and Geneva, New York, to the other colonies where all individuals are of intermediate nature. In between there are three possible recombinations. (1) A mixed colony of pure *latifolia* and pure *angustifolia* and no intermediates. This was not observed but such a combination is approached at Gary, Indiana, Portage and Theresa, Wisconsin, and Saugatuck, Connecticut; (2) A colony with pure *latifolia* individuals, pure *angustifolia* individuals and intermediates between the two. Examples of this may be seen at Pickett and Fond du Lac, Wisconsin, Marmora, Ontario, Lordship and Sherwood Island, Connecticut, and Newcastle, Maine; (3) In the most common type of colony one species is predominant but many individuals show one or more characteristics of the other species. An extreme case is at Stony Point, Connecticut, where all but two of the twelve individuals of *T. angustifolia* have the dark brown or black spike of *T. latifolia.* At Compo Beach, Connecticut, the majority of individuals are close to *T. angustifolia,* but have the knobless hairs of *T. latifolia.* Conversely, most individuals from Black River Falls, Adams and Poynette, Wisconsin, show the lighter colored spike characteristic of *T. angustifolia* in colonies where *T. latifolia* characters predominate. To any person familiar with cat-tails in the field, a possible explanation suggests itself—that many individuals have been collected from a single clone. Clones do vary in extent and may even mix in the same territory, so there is a possibility of duplicating collections from a clone. However, at Stony Point, Connecticut, the clones were more or less distinct from each other and looked different. At Compo Beach individuals were collected from a large swamp through the middle of which ran a stream with a sandy-gravel bottom. Since this stream was shallow and offered good footing the collector took specimens about every twelve feet on alternate sides of the stream. Further evidence against much duplication is seen in those colonies where, for example, the spike of the dark *latifolia* color is present throughout, but variations of other characteristics show that many clones are represented.

Ecology, and Observations on Specific Areas

The edaphic conditions tolerated by *T. latifolia* range from basic to acid waters, while *T. angustifolia* is mostly in basic waters and will tolerate some salinity, as in the salt marshes along the east coast. Where there is an overlap in these habitats, hybrid swarms are found.

In Wisconsin the soils to the south and east are, in general, limy, while those of the north and northwest are derived from granite and sandstones. This is reflected in figure 6, where the occurrence of *T. angustifolia* characters is concentrated southeastward. This may represent a recent infusion of *T. angustifolia* into a previously established population of *T. latifolia,* for there is no evidence of the presence of *T. angustifolia* until recently. It is impossible to demonstrate the former absence of *T. angustifolia* in southeastern Wisconsin; however, only *T. latifolia* was listed from Madison by Cheney and True (1893), who stated that it was "common in marshes, especially east of the city of Madison," where *T. angustifolia* is now abundant. J. H. Schuette, a remarkably prolific collector about Green Bay in the last decade of the Nineteenth Century, got only *T. latifolia* (specimen in Chicago Natural History Museum). Our oldest collections of *Typha* from southeastern

Wisconsin are pure *T. latifolia* (Milwaukee, about 1870, Lapham; Janesville, 1890, Skavlem; Racine, 1906, Heddle 253a).

Further correlation between soil type and species is seen in central New York state in the Finger Lake region. Here the soil is derived from glacial till of limestone and calcareous shale. Near Geneva on Lake Seneca stands a practically solid colony of *T. angustifolia.* From Chittenango and to the east at Palatine Bridge and Avon, New York, where intermediates are found, the soil has less lime content.

In southern New York and New England the soils are largely acidic in nature, being derived from weathered sandstone and shale, and from glacial till and outwash materials from granitic and gneiss parent rock (U.S.D.A., 1938). Here again *T. latifolia* is dominant except in the areas where the water is, or has recently been, somewhat saline. In the region of overlap, in the salt marshes on the Connecticut coast, intermediates occur.

Taxonomy and Nomenclature

It is natural that the occurrence of many types of intermediates, with various recombinations of characters, should have had its reflection in the taxonomy of the group. The following names are among those that appear in North American literature. Several other names, applied to plants in regions where *T. domingensis* enters the scene, are not here considered.

T. glauca Hotchkiss and Dozier, Amer. Midl. Nat., **41**: 237–254, 1949; perhaps Godron, Flore de Lorraine, **3**: 20, 1844, and other European authors. As described by Hotchkiss and Dozier, this has 2 characters of *T. angustifolia* (usually a gap in the spike; pistillate portion of spike not black-mottled), and 4 characters of *T. latifolia* (pistillate bracts usually absent, stigma flattened, aborted pistil club-shaped, and pistillate hairs not knobbed). Scattered individuals with this combination of characters appears in mass collections from northeast of Black River Falls, and Sheboygan, Wisconsin (fig. 6) and from Cedar River, Michigan (fig. 5). *T. glauca* is described as being larger throughout than *T. angustifolia,* particularly in respect to the spikes.

T. angustifolia var. *elongata* (Dudley) Wiegand, Rhodora **26**: 1. 1924, and *T. angustifolia* var. *longispicata* Peck, Rep. N. Y. State Bot., **47**: 36. 1894. These, also, appear to be large extremes of *T. angustifolia.* Whether or not introgression from *T. latifolia* is a factor in producing the large size would be difficult to say.

T. angustifolia var. *calumetensis* Peattie, Amer. Midl. Nat., **10**: 129. 1926. Of the cited specimens, only no. 2340 has been examined in the Chicago Natural History Museum. It is a characteristic individual of *T. angustifolia* except for the club-shaped aborted pistil.

Summary

In many parts of the northern United States and southern Canada *Typha latifolia* and *T. angustifolia* occupy the same region and may often be found in the same colony. Mass collections have been made, consisting of a spike and a leaf from each clone in a colony (or from each clone that could be conveniently reached). Six pairs of qualitative characters have been used in the analysis of these collections. The gap between the pistillate and staminate portions of the spike present in *T. angustifolia* and absent in *T. latifolia,* and the light brown spike typical of *angustifolia* and the mottled black spike of *latifolia,* while reasonably constant for the respective "pure species," seem to diffuse readily from one species to the other in regions of coexistence.

The other four characters include the slender bract subtending the pistillate flower, present in *T. angustifolia* and absent in *T. latifolia*; the filiform stigma of *T. angustifolia* and the flattened stigma of *T. latifolia*; the flattened and flabellate aborted pistil of *T. angustifolia,* and club-shaped aborted pistil of *T. latifolia*; the presence of knobbed hairs on the pistillate flower of *T. angustifolia* and the knobless

hairs on the pistillate flower of *T. latifolia*. These characters are much more closely correlated, but there is nevertheless some diffusion of these characters from one species to the other.

Of the 821 individuals represented, on the basis of these 6 characters, 536 are pure *T. latifolia*, 86 are pure *T. angustifolia*, and the rest show various recombinations of the characters of the two. It is concluded that while there has been introgression where the two species occur together, there are forces, both external and internal, tending to maintain them as specific entities.

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HYBRIDIZATION AND GRAFTING IN SPECIES OF *THEOBROMA* WHICH OCCUR IN AMAZONIA

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INTRODUCTION

Beginning in 1945, the authors have carried out a series of experiments on hybridization of species of *Theobroma* which occur in the basin of the Amazon. The cultivated cacao tree (*Theobroma cacao*) has been used frequently in these experiments, the original purpose having been an attempt to transfer various desirable characters of the wild species into the cultivated form, as suggested by Posnette (1945), who first succeeded in obtaining some cross-pollinations between species of *Theobroma*. Experiments have also been made on reciprocal grafting between the various species. These experiments have revealed an interesting parallelism between the behavior of some species in hybrids and in grafts. The purpose of the present article is to present a summary of the results obtained in our *Theobroma* work to date.

THE PARENTAL FORMS

In his revision of the genus *Theobroma*, Ducke (1940) recognizes nine species which occur in Amazonia. Considered morphologically, these species fall into several groups. Thus, *T. Mariae* and *speciosum* have flowers on the trunks only, *T. microcarpum, grandiflorum, subincanum, obovatum,* and *bicolor* produce flowers only on branches, while *T. cacao* and *Spruceanum* produce them both on trunks and on branches. Seeds of *T. Mariae* germinate in 30 or more days, while those of other species take only 15 days to germinate. The branching of most species is trichotomous, but in *T. Mariae* it is monopodial, and in *T. cacao* it is in fives. Axillary buds on the branches are absent in *T. speciosum, Spruceanum, bicolor* and *cacao*, and present in the other species. In *T. speciosum, Spruceanum, bicolor* and *cacao*, the stem arises from buds below the branching points while in the other species it arises from axillary buds on the branches. *T. cacao* is somewhat variable with respect to the above trait, since some branches develop buds which give rise to a secondary stem. Furthermore, *T. cacao* is the only species which is capable of base sprouting, even in adult trees.

The leaves are digitate in *T. Mariae*, while the leaves of the other species are entire. Young plants of *T. bicolor* have cordiform leaves. Young leaves are green in *T. Mariae, speciosum, Spruceanum, bicolor* and *microcarpum*, and either green or purple in the other species. The hybridization experiments have shown that the green color is a single recessive trait, purple being dominant. Accordingly, we have whenever possible used plants with green foliage as female parents, and those with purple foliage as male parents. This permits ready detection of the possible contaminations. Leaves of *T. Mariae, subincanum, obovatum* and *grandiflorum* are hairy; the adult leaves of *T. Mariae* have the further characteristic of not losing their hairs when rubbed against human hands.

The morphological and gross physiological traits thus shed relatively little light on the relationships of the nine species considered. It is clear only that *T. Mariae* is a very distinct form, and indeed it is placed in a separate subgenus or section Herrania (Ducke, 1940), which some authors consider to be a separate genus (Shultes, 1945).

The Species Crosses

The techniques used in the hybridization experiments have been described elsewhere (Addison and Tavares, 1952). Here it will be sufficient to note that different individual trees of the same species may vary with respect to the ease with which they produce hybrids with other species when used as female parents in crosses. Thus one tree of *T. cacao* growing in the garden of the Museum Paraense "Emilio Goeldi," at Belém, proved most favorable for our purpose, and was subsequently used more than were other trees.

The results of the cross-pollination of the species of *Theobroma* are summarized in table 1. In this table the name of the species used as the mother is always given first, that of the father second. It is clear at a glance that most combinations of species produce no offspring. It should be noted that this inability to produce hybrids is not due to failure of germination of the pollen or to failure of the pollen tube growth, as has been verified by special observations. An attempt to improve matters by application of 0.1% to 0.25% alfanaphtalene acetic acid lanoline at the point of abscission of the flowers gave no positive results.

The only species which, when used as a female, is able to produce hybrid seeds with most of its congeners is the cultivated *T. cacao*. Only the cross *cacao* × *Spruceanum* has consistently failed, and *cacao* × *bicolor* produced a single ripe fruit with few seeds. On theoretical grounds, it is perhaps suggestive that the isolating mechanisms which exclude interspecific crosses should be weakest in the

TABLE 1. *Numbers of pollinations made, of fruits obtained, of seeds in the fruits, and the frequency of seeds which germinated in various interspecific crosses in the genus* Theobroma

Species	Pollinations	Fruits	Seeds	Germination
cacao × *speciosum*	375	24	224	0
cacao × *Mariae*	397	52	191	0
cacao × *microcarpum*	489	7	11	20%
cacao × *obovatum*	674	45	few	0
cacao × *grandiflorum*	999	285	548	40%
cacao × *subincanum*	375	24	few	0
cacao × *bicolor*	381	1	few	0
cacao × *Spruceanum*	2,239	0	0	0
bicolor × *speciosum*	293	0	0	0
bicolor × *Spruceanum*	556	0	0	0
bicolor × *obovatum*	520	0	0	0
bicolor × *subincanum*	250	0	0	0
bicolor × *cacao*	2,440	0	0	0
bicolor × *Mariae*	641	0	0	0
grandiflorum × *cacao*	745	0	0	0
grandiflorum × *bicolor*	462	0	0	0
grandiflorum × *Spruceanum*	743	0	0	0
grandiflorum × *speciosum*	541	0	0	0
grandiflorum × *microcarpum*	654	0	0	0
grandiflorum × *Mariae*	531	0	0	0
grandiflorum × *obovatum*	465	37	701	77%
grandiflorum × *subincanum*	317	39	514	72%
subincanum × *microcarpum*	259	0	0	0
subincanum × *Mariae*	550	0	0	0
subincanum × *speciosum*	690	0	0	0
subincanum × *Spruceanum*	505	0	0	0
subincanum × *grandiflorum*	189	42	756	65%
subincanum × *obovatum*	515	136	1,632	High

TABLE 1.—*Continued.*

Species	Pollinations	Fruits	Seeds	Germination
obovatum × *cacao*	246	0	0	0
obovatum × *Mariae*	194	0	0	0
obovatum × *microcarpum*	581	0	0	0
obovatum × *Spruceanum*	527	0	0	0
obovatum × *grandiflorum*	506	0	0	0
obovatum × *subincanum*	539	0	0	0
speciosum × *cacao*	1,011	0	0	0
speciosum × *bicolor*	1.264	0	0	0
speciosum × *Mariae*	1,896	0	0	0
speciosum × *grandiflorum*	660	0	0	0
speciosum × *Spruceanum*	437	72	1,406	63%
speciosum × *obovatum*	25	0	0	0
Spruceanum × *cacao*	159		0	0
Spruceanum × *bicolor*	97	0	0	0
Spruceanum × *microcarpum*	102	0	0	0
Spruceanum × *grandiflorum*	102	0	0	0
Spruceanum × *Mariae*	13	0	0	0
Spruceanum × *subincanum*	101	0	0	0
Spruceanum × *obovatum*	102	0	0	0
Spruceanum × *speciosum*	41	32	62	52%
microcarpum × *cacao*	395	0	0	0
microcarpum × *bicolor*	161	0	0	0
microcarpum × *grandiflorum*	500	0	0	0
microcarpum × *Mariae*	490	0	0	0
microcarpum × *obovatum*	500	0	0	0
microcarpum × *subincanum*	187	0	0	0
microcarpum × *speciosum*	176	0	0	0
microcarpum × *Spruceanum*	1,786	0	0	0
Mariae × *microcarpum*	353	0	0	0
Mariae × *Spruceanum*	426	0	0	0
Mariae × *speciosum*	235	0	0	0
Mariae × *obovatum*	1,214	0	0	0

most extensively cultivated species. Hybrid seeds are produced in the crosses *subincanum* × *grandiflorum* and the reciprocal, *speciosum* × *Spruceanum* and the reciprocal, *grandiflorum* × *obovatum*, and *subincanum* × *obovatum*. Reciprocals of the two last named crosses have so far failed to give hybrid seeds. It must however be noted that *obovatum* is, in contrast to other species with the exception of some *cacao* strains, self-fertile, and this fact makes the hybridization work with this species especially difficult. *T. bicolor*, when pollinated by *cacao*, *speciosum*, and *Spruceanum*, gives fruits which do not reach maturity but fall off after growing to about 10 cm. in length. It may be noted that the abscission of the fruits is a characteristic of the species *bicolor*, but in *bicolor* it takes place when the fruits are ripe. In the reciprocal crosses, the fruits attain no more than 3 cm. in size, and die off.

Obtaining hybrid seeds does not insure production of hybrid plants because of the deficient germination of the seeds, as indicated in table 1. The seeds of the pure species give, in most cases, between 90% and 100% germination.

THE F_1 HYBRIDS

As shown above, only some of the many species combinations have produced viable

hybrid seeds. The characteristics of the hybrids obtained are as follows.

T. grandiflorum × *T. obovatum.* In 1949, several hundred hybrid seeds germinated in baskets with sandy soil. Many of the seedlings were transferred in a lath house. Of these, 7 died, 7 are at present (1952) dwarfs or semi-dwarfs, and 22 grew normally. Other seedlings (328) were transplanted in the field; only 50 of them are alive at present. The slow growing hybrids, and some of the normally growing ones, show a characteristic necrosis of the tips of the leaves, and sometimes of as much as a half of the leaf blade. Only 14 hybrid plants appear to be normal both with respect to the growth and of the condition of the leaves.

Seven pollinations were made using the F_1 hybrids as mothers and *T. obovatum* as father. No fruits were obtained. A total of 103 pollinations of the hybrids by the pollen of *T. grandiflorum* gave 63 fruits, 20 of which matured and produced 354 seeds, most of which germinated successfully. Of the 135 pollinations with hybrid pollen on *T. grandiflorum* stigmas, only 8 gave fruits with a total of 161 seeds. These seeds also germinated successfully. The backcross to *T. obovatum* as mother has not matured yet.

The fruits produced by the hybrid plants are, on the average, 78 mm. long and 44 mm. in diameter; in *T. obovatum* the corresponding dimensions are 51 × 34 mm., and in *grandiflorum* 158 × 92 mm. A hybrid fruit contains, on the average, 12 seeds, while the parents have respectively 6 and 38 seeds. The taste of the hybrid fruit is likewise intermediate between the parents. So is the external appearance of the surface of the fruits. A trait which is dominant rather than intermediate in the hybrids is the falling off of the mature fruits from the tree, which also occurs in *grandiflorum.*

T. grandiflorum × *T. subincanum.* This cross produces seeds which germinate well and give seedlings that are normally viable. In 1949, a total of 45 hybrid seedlings were planted in a lath house. They grow quite normally, and do not show the necrosis of the leaves observed in the *grandiflorum* × *obovatum* hybrids (see above). The hybrids, like the *subincanum* parent, have the young stems flexible and nodding until hardened: the *grandiflorum* parent does not show this trait. These hybrids have flowered in 1952. The appearance of the flowers in the hybrids is intermediate between the parental species.

T. subincanum × *T. grandiflorum.* These hybrids are not appreciably different from the preceding ones.

T. subicanum × *T. obovatum.* This cross also produces good seeds and viable seedlings. In 1949, 56 seedlings were planted in the lath house. The hybrids are about as small as the *obovatum* parents of corresponding age. Some of the hybrid plants show disturbances in the formation of the leaves but others appear to be perfectly normal. Only three hybrid trees have flowered to date; their pollen grains appeared to be normal in the iodine solutions. Attempts to obtain a backcross progeny by pollinating the hybrids with *subincanum* pollen gave, so far, no fruits. Some fruits have nevertheless been obtained by using the pollen of a third species, *grandiflorum.*

T. Spruceanum × *T. speciosum.* The 35 seedlings which germinated in 1949 were planted in a lath house and gave rise to apparently healthy trees. The parental species are rather similar in appearance of the leaves and in their general habitus; with respect to whatever differences can be noted between them, the characteristics of *speciosum* seem to be dominant in the hybrids. Thus far 5 hybrids have flowered; the flowers are intermediate between the parents. Pollination with *Spruceanum* pollen gave rise to many fruits which, however, failed to grow beyond about 2.5 cm. in length. This may be due to the youth of the hybrids. It may be noted that *Spruceanum* flowers at the age of about 1½ years, while *speciosum* reaches flowering when 5 or more years old. The early flowering trait is then, dominant in the hybrids.

TABLE 2. *The numbers of grafts made (the upper figures in each cell), of grafts that took (the lower figures), and development of the scions in species of Theobroma*

N—the scion grows normally; SN—subnormal growth of the scion; M—the scion becomes about 30 cm. long and then dies off; F—the scion develops some leaves and then dies; D—the scion dies soon after the beginning of growth.

Stock ↓ \ Scion →	*cacao*	*bicolor*	*grandiflorum*	*speciosum*	*subincanum*	*Spruceanum*	*microcarpum*	*Mariae*	*obovatum*
cacao	20	20	34	50	34	20	30	20	34
	16	9	20	28	18	15	20	2	18
	N	M	F	M	F	M	SN	D	M
bicolor	35	20	35	40	35	20	35	35	40
		19	11	22	20	15		15	4
	D	N	D	SN	D	SN	D	D	D
grandiflorum	24	20	20	40	23	20	20	20	23
	4	4	8	10	8	9	6		9
	F	F	N	SN	N	F	D	D	N
speciosum	35	20	35	40	35	20	35	35	39
		17	7	31	3	19		9	
	D	N	D	N	D	N	D	D	D
subincanum	24	25	20	25	20	25	24	25	25
	24	23	17	22	15	16	13	13	11
	F	D	N	M	N	M	D	D	N
Mariae	20	20	20	20	20	20	20	20	20
	3	3	15	20	13	10		20	18
	D	F	F	F	F	F	D	N	F
obovatum	20	20	20	20	20	20	20	20	20
	18	16	17	6	19	13	10	2	13
	D	F	N	F	N	M	D	D	N

T. speciosum × *T. Spruceanum*. These hybrids were planted in the field and developed into trees which resemble those of the preceding cross which grow in the lath house. Thus far only a single tree has flowered.

T. cacao × *T. grandiflorum*. As shown in table 1, this cross gives rise to many hybrid seeds, although the number of seeds per fruit is lower than that in pure *cacao*. The germination of the hybrid seeds is nevertheless poor, and few seedlings reach as much as 15 cm. in height. Those hybrid seedlings which grow push the cotyledons out of the soil, resembling in this respect the *cacao* parent. No hybrids have grown anywhere near the flowering stage.

GRAFTING

Experiments were made grafting the buds from the stem of one species to that of another individual of the same or of a different species. The results are summarized in table 2.

It can be seen that all the intraspecific grafts that take develop normally. Among the interspecific grafts much variation is observed. The three species *grandiflorum*, *obovatum*, and *subincanum* can be grafted reciprocally with ease. The scion of *grandiflorum* and *subincanum* gave dwarf trees when grafted on *obovatum* stocks, since *obovatum* is the smallest of the three species. *Speciosum* can also be grafted on *grandiflorum*; one of the grafts has attained 120 cm. in height, but died there-

after. Another well defined group are *bicolor, speciosum,* and *Spruceanum,* although *bicolor* is less closely related to the other two than the latter are to each other. When *bicolor* is used as scion and *speciosum* as stock, some grafts develop a callosity at the locus of the graft, which has a tendency to sprout roots. *Spruceanum* is a smaller plant than its two relatives, and when it is grafted on *speciosum,* the scion grows more vigorously than it does on its own roots. The scions of *microcarpum* develop fairly normally on *cacao.*

Discussion

The data presented above demonstrate the existence, in *Theobroma,* of a far reaching, although by no means perfect, correlation between the outcomes of hybridization and of grafting experiments. In general, the species which produce hybrid progenies, or at least hybrid seeds, can be grafted successfully onto each other. Vice versa, where the interspecific grafts die off hybridization is usually impossible. Thus, the three species, *T. subincanum, grandiflorum,* and *obovatum,* can exchange grafts freely, all nine possible combinations of scions and stocks giving normal growth (table 2). *Subincanum* and *grandiflorum* also produce viable hybrids, the reciprocal crosses being alike; *obovatum* crosses freely with the two other species when used as a male parent, but not as a female (table 1). Normal or subnormal growth is also observed in reciprocal grafts of the three species *speciosum, Spruceanum* and *bicolor.* Of these, *Spruceanum* and *speciosum* can be crossed in either direction, but *bicolor* gives no hybrid seeds with either of the two other species. The scions of *microcarpum* grow reasonably well on *cacao,* and the cross *cacao* × *microcarpum* does not give a viable progeny, as the reciprocal one.

Whether the success of hybridization on the one hand, and the outcome of grafting on the other, have a common physiological basis is a matter of speculation. However that may be, the data at our disposal permit the following division of the nine *Theobroma* species into four groups:

I	II	III	IV
subincanum	*cacao*	*speciosum*	*Mariae*
grandiflorum	*microcarpum*	*Spruceanum*	
obovatum		*bicolor*	

This classification, based on experimental data, agrees with, or at least is not contradicted by, the morphology of the species concerned.

In conclusion, it may be pointed out that the species of *Theobroma* are remarkable by the completeness of the reproductive isolation which prevents the gene exchange between them. Hybridization of these species in their natural habitats is less probable than that of species of many other genera of plants. The rather extensive field work of the authors and of their colleagues in different parts of Amazonia has thus far failed to detect any natural hybrids between species of *Theobroma.*

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Summary

Experiments have been made intercrossing the nine species of *Theobroma* which occur in *Amazonia.* Most cross pollination gives no normally maturing fruits, but some crosses result in production of hybrid seeds. Hybrid seeds germinate in some cases with difficulty, and the seedlings often show a lowered viability. Only some adult hybrids have been obtained, but these have proved at least partly fertile. Buds of some species when grafted onto others fail to develop, while in other combinations of species the scions grow normally. The degrees of success of interspecific hybridization and of grafting show a strong positive correlation. A classification of the nine species based on the experimental data is proposed.

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ONTOGENETIC AND EVOLUTIONARY ALLOMETRY[1]

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INTRODUCTION

The insight that changes in proportion connected with increase of body size are a major factor in evolution (cf. Bertalanffy, 1942, 1951; Rensch, 1947), has lent a deeper significance to studies on the relative growth of organs. Relative growth can be considered either with respect to development, *i.e.*, comparing individuals of the same species and different age and size; or with respect to evolution, *i.e.* comparing adult individuals of related species (Hersh, 1941). In general, ontogenetic as well as evolutionary relative growth follows the law of allometry (Huxley, 1932).[2] However, notwithstanding the great number of investigations on allometry, the question of the relation between ontogenetic and evolutionary allometry is rather little studied. The problems involved were envisaged especially in the recent work by Rensch (1948, a, b) who, however, gives a large amount of interspecific, but few intraspecific data. The present study is a contribution to the problem of the connection between both kinds of allometry.

ALLOMETRIC GROWTH OF SOME ORGANS OF THE RAT

The data presented here were obtained in connection with an investigation on the relation between tissue respiration and body size (Bertalanffy and Pirozynski, 1951, and work in press; Pirozynski and Bertalanffy, 1951).

Male and female albino rats (Wistar strain) were used. All animals were killed by breaking the cervical vertebrae. The organs, *i.e.* heart, liver, thymus, lungs, kidneys, and brain, were immediately removed and placed in ice cold saline as necessary for the Warburg technique. The larger blood vessels and nerves as well as the connective tissue were carefully removed from the organs, especially from lungs, heart, and brain. All organs were dried by gentle touching with hard filter paper prior to weighing in order to remove the blood and saline. Coagulated blood in the heart ventricles was removed by means of a fine forceps.

The facts that the preparations were made in accordance with the needs of the Warburg technique (transfer of the organs into saline and storing in ice), and that the factor of age was not considered (animals of equal body weight may, of course, be of different age), may partly account for the range of variations. Variability might be less if the determinations had been made with the sole purpose of determining organ weight.

[1] Supported by grants from the National Research Council and the National Cancer Institute of Canada.

[2] Since the terminology of relative growth has been subject to many discussions, it may be advisable to define the terms as used in this paper. *Allometry* is the relative increase of a part of an organism (in the widest sense, including morphological, biochemical components, physiological characteristics, etc.) with respect to the size of the body (or another part), and following the power formula (1). The terms *intraspecific* and *interspecific* are self-explaining. Intraspecific allometry is *ontogenetic* insofar as growing animals of different size are compared. If interspecific allometry is called *evolutionary*, this does not necessarily imply that the forms under consideration represent a phylogenetic series. Evolutionary allometry in this narrower sense can be established only in the relatively few cases where the phylogenetic relations are sufficiently known (*e.g.* evolutionary allometry in horses: Robb, 1935–37; in titanotheres: Hersh, 1934). In the wider sense, as used in this paper, evolutionary allometry signifies the relative increase of organs connected with the increase of body size as found in series of mammals. Ontogenetic relative growth is also called *heterauxesis*, while for absolute-size allometry (comparison of organisms of corresponding stage, usually adults, but of different groups as races, varieties, species, genera) the term *allomorphosis* is used (Needham and Lerner, 1940; Huxley, Needham and Lerner, 1941; Reeve and Huxley, 1945, p. 123) which, for our present purposes, corresponds to evolutionary allometry.

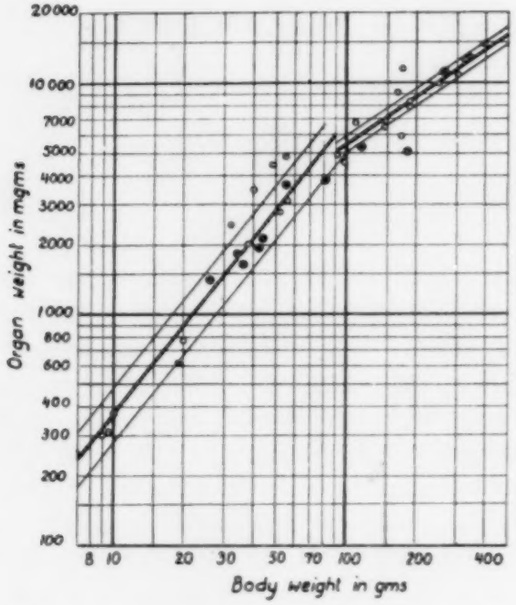

FIG. 1. Relative growth of the liver in albino rats. In this, as in the following figures, the heavy line indicates the logarithmic regression, the two paralleling lines, the standard error in per cent, including 2/3 of the cases. ○ = males, ● = females.

Organ growth in the rat was studied in classical papers by Hatai (1913), Jackson (1913), and Donaldson and Hatai (1931) (cf. also Donaldson, 1924, Tables 144–146). The observations to be presented here essentially confirm these older results, but offer some new points of view.

Our data are calculated according to the allometry equation:

$$y = bx^{\alpha}$$

(y = weight of organ, x = body weight, α, b constants), giving a straight line in the log-log plot. The statistical evaluation of the data, including the calculation of the allometry exponent α, the integration constant b, the standard error $S_{(\log y \cdot \log x)}$, and the correlation coefficient ρ, was made according to the method indicated by Brody (1945, p. 398 ff.).

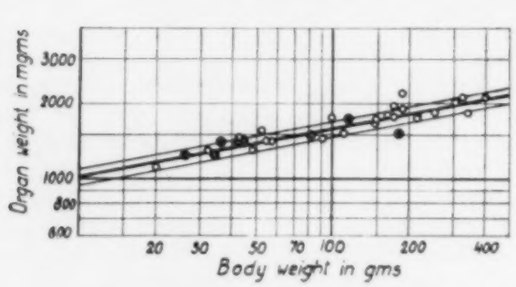

FIG. 2. Relative growth of the brain in albino rats.

Our results are given in figures 1–6, and table 1. All organs under consideration show negative allometry in relation to body size, although to a different extent. A comparison of a number of data,

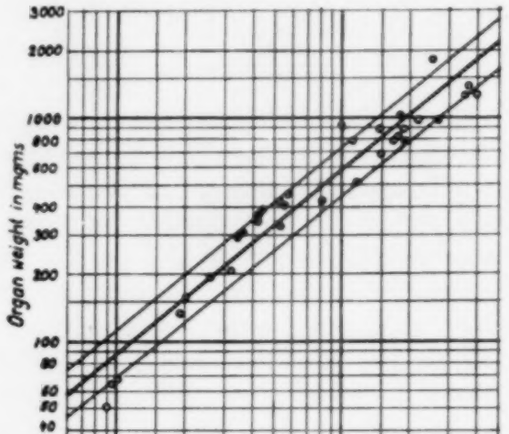

FIG. 3. Relative growth of the heart in albino rats.

intraspecific and interspecific, is given in table 2. This table illustrates the fact that, suitable methods presupposed, the values obtained by different observers and in different series of animals are practically identical or, in other words, that the allometry exponent is a reproducible con-

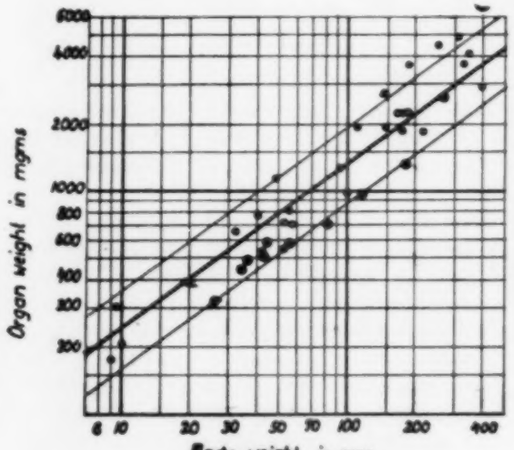

FIG. 4. Relative growth of the lungs in albino rats. There might be a slight sexual difference in the relative growth of the lungs since the data could be represented by two regression lines of equal slope (α), but with b somewhat lower for the females than for males.

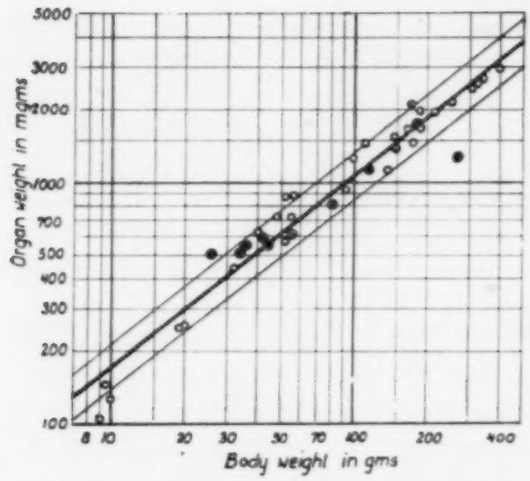

FIG. 5. Relative growth of the kidneys in albino rats.

stant characteristic of a certain group. On the other hand, inconsistencies indicate that either the standards of measurement were different, or else that the reliability of the data is doubtful. Some remarks may be made with respect to particular organs.

Liver. Apart from the thymus, which undergoes involution after the growth period, the liver is the only one among the organs studied here to show an obvious break in the allometric curve, occurring at about 100 gm. body weight (fig. 1). The reality of this break seems to be without doubt, since it is found in Hatai's data (1913) and Brody's plot (1945), as well as in our data. This size corresponds

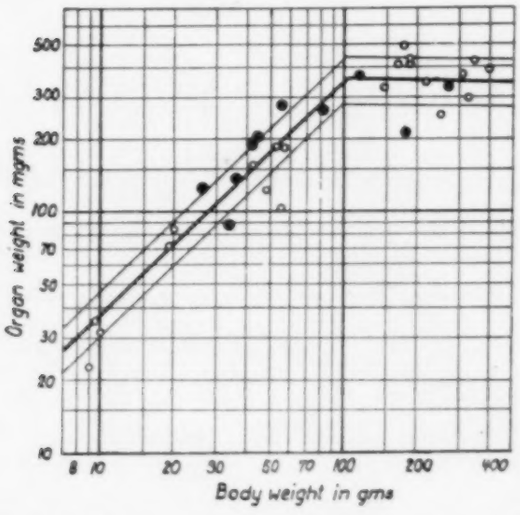

FIG. 6. Relative growth of the thymus in albino rats.

to the period of beginning puberty. It appears that a number of diverse but interrelated changes occur at this time:

1) There seems to be in this region the transition from the first to the second cycle of total growth (Bertalanffy, 1938, 1951).

2) The allometry of basal metabolic rate with respect to body size also shows a break in this region (Bertalanffy and Racine, unpublished).

3) A corresponding break is found in the tissue respiration of liver (Bertalanffy and Pirozynski, in press). Also with respect to tissue metabolism, the liver is (apart from the thymus) the only organ investigated to show a break in the allometric plot of the Q_{O_2} values which corresponds to the break in the allometric growth of the organ.

4) There is, of course, the involution of the thymus (fig. 6), and a corresponding break is found in the tissue respiration of the thymus (Bertalanffy and Pirozynski, in press).

TABLE 1. *Relative growth of some organs in the albino rat*

	N	a	b	$S_{(\log y \cdot \log x)}$	ρ
Liver					
1st cycle	22	1.264	20.31	0.117	0.957
2nd cycle	17	0.670	24.75	0.029	0.770
Brain	32	0.197	655.90	0.026	0.946
Heart	35	0.816	13.32	0.1024	0.967
Lungs	39	0.726	45.14	0.174	0.896
Kidneys	39	0.796	27.32	0.090	0.972
Thymus					
1st cycle	17	0.954	4.092	0.086	0.965
2nd cycle	14	0.022	3.984	0.099	0.035

A difference in the relative growth of the liver with respect to sex, as stated by Rensch (1948 a, p. 350), is not found in our data.

Brain. The brain is the organ probably studied most with respect to its relative growth, and there is a great number of different interpretations (Snell, Lapicque, Dubois, Brummelkamp, von Bonin, Count, Portmann, and others; review and discussion: Bertalanffy, 1951, pp. 338 ff.).

TABLE 2. *Intraspecific and interspecific allometry (α-values) of some organs in mammals*

	Rat							
	Present data	Brody's calculation	Cat	Dog	Monkey	Steers	Horse	Mature mammals interspecific
Brain	0.20	0.17[1]		0.25[5] 0.25[6]	0.62[9]	0.30[10]	0.24[13]	0.66[17] 0.69[18] 0.58[19] 0.54[21]
Heart	0.82	0.80[2]	♂ 0.92[3] ♀ 0.82[3]	1.00, 0.86, 0.93[7]	0.69[9]	0.93[11]		0.83[20] 0.82[19] 0.85[21] 0.84[22] 0.98[18]
Lungs	0.73	0.75[2]		0.82[8]	0.92[9]		0.58[14]	0.98[19] 0.99[18]
Liver	1st cycle: 1.26 2nd cycle: 0.67	1st cycle: 1.14[2] 2nd cycle: 0.68[2]		0.71[8]		0.70[12]	0.61[15]	0.87[18] 0.88[22] 0.92[19]
Kidneys	0.80	0.82[2]	♂ 0.65[4] ♀ 0.61[4]	0.70[8]			0.66[16]	0.85[18] 0.87[19] 0.76[22]

[1] Donaldson, H. H., and S. Hatai. 1931. J. Comp. Neurol., **53**: 263. Calculation by Brody (1945): p. 592.

[2] Hatai, S. 1913. Amer. J. Anat., **15**: 87. Calculation by Brody (1945): pp. 597, 625, 626, 627.

[3] Van Liere, E. J., and C. K. Sleeth. 1931. Unpublished data, Univ. West Virginia. Calculation by Brody (1945): p. 597.

[4] Hall, V. E., and W. W. MacGregor. Unpublished data. Calculation by Brody (1945): p. 625.

[5] Lapicque, L. 1898. C. R. Soc. Biol., **50**: 784. Calculation by Brody (1945): p. 592.

[6] Klatt, B. 1949. Biol. generalis (Wien), **19**: 51.

[7] Van Liere, E. J., and C. K. Sleeth. 1931. Unpublished data, Univ. West Virginia. Stewart, G. N. 1921. Amer. J. Physiol., **58**: 45. Calculation by Brody (1945): p. 597.

[8] Stewart, G. N. 1921. Amer. J. Physiol., **58**: 45. Calculation by Brody (1945): pp. 625, 626, 627.

[9] Hrdlicka, A. 1925. Amer. J. Anthropol., **8**: 202. Calculation by Brody (1945): pp. 592, 597, 627. Hrdlicka gives data for different species of monkeys. It is not apparent upon which species Brody's calculation is based.

[10] Missouri data. Calculation by Brody (1945): p. 592.

[11] Moulton, C. R., P. F. Trowbridge, and L. D. Haigh. 1922. Missouri Agr. Exp. Sta. Res. Bull., **54**: 48. Calculation by Brody (1945): p. 597.

[12] Missouri data. Calculation by Brody (1945): p. 626.

[13] Crile, G., and D. P. Quiring. 1940. Ohio J. Sci., **40**: 219. Calculation by Brody (1945): p. 592

[14] Crile, G., and D. P. Quiring. 1940. Ohio J. Sci., **40**: 219. Calculation by Brody (1945): p. 627.

[15] Crile, G., and D. P. Quiring. 1940. Ohio J. Sci., **40**: 219. Calculation by Brody (1945): p. 626.

[16] Crile, G., and D. P. Quiring. 1940. Ohio J. Sci., **40**: 219. Calculation by Brody (1945): p. 625.

[17] Bonin, G. von. 1937. J. gen. Psychol., **16**.

[18] Brody, S. 1945. Bioenergetics and growth. New York: pp. 592, 596, 625, 626, 627.

[19] Quiring, D. P. 1939. Growth, **2**: 335 (Ungulates).

[20] Klatt, B. 1919. Biol. Zbl., **39**: 406.

[21] Quiring, D. P. 1941. Growth, **5**: 301–327.

[22] Rensch, B. 1948. Zool. Jb. (Physiol.), **61**: 337.

It appears that, at least in the sense of a rough-and-ready formula, evolutionary allometry in the series of mammals is surface-proportional ($\alpha = 0.66$), as was already contended by Snell and demonstrated by von Bonin (1937). Klatt (1949, p. 54), whose work on relative growth (since 1919) is pioneering, is of the opinion that, as far as intraspecific allometry is concerned, only the data on Man (Dubois) and on dogs (Klatt) are reliable. These data give the intraspecific Dubois exponent $\alpha = \frac{2}{9}$ (for the dog, according to Klatt $\alpha = 0.25$). Our data for the rat (fig. 2, $\alpha = 0.20$) correspond well to this exponent.

Heart. The intraspecific exponent for the rat is 0.82 (fig. 3). Interspecifically, a similar exponent was found by different authors (Klatt, Quiring, Rensch), while a much higher exponent (0.98) is stated by Brody. The reason for this discrepancy is not obvious.

Discussion

A comparison of allometries in mammals, intraspecific and interspecific, as given in table 2, illustrates an important fact. Ontogenetic allometry (heterauxesis) does not necessarily correspond with interspecific allometry (allomorphosis). This corresponds to Rensch's conclusions (1948a, p. 386, 1948b), but is confirmed on a broader basis by the data given above. We must ask what is the meaning of this fact.

It appears that a certain quantitative ratio between the organs is necessary for the proper functioning of the organism. This is expressed by the fact that the law of allometry applies in interspecific comparison, *i.e.* to adult animals of different species. This signifies that the organs concerned always stand in a certain proportion to body size, as expressed by the allometry exponent α. To some extent, the values of the allometry constants of organs are intelligible. Basal metabolic rate is proportional, in the series of adult mammals "from the rat to the elephant," rather to the $\frac{3}{4}$ power ($\alpha = 0.75$) than to the $\frac{2}{3}$ power ($\alpha = 0.67$) of weight, the latter corresponding to the classical surface rule of metabolism (Brody, 1945; Kleiber, 1947). It is understandable, therefore, that organs like kidney, liver, and heart, will increase to correspond with the demands of metabolism, plus an allowance as safety-factor, that is, with an exponent somewhat greater than 0.75. In the lung, gas exchange takes place on the surface. It must grow proportional to weight in order that surface (which, neglecting anatomical and histological changes, would increase as a $\frac{2}{3}$ power of weight) is increased in such a way as to guarantee an oxygen supply necessary if metabolism follows the surface (or $\frac{3}{4}$ power) rule. Accordingly, the interspecific allometry exponent of the lung is approximately 1. As far as the brain is concerned, Dubois's conception may be mentioned that the relations with environment which determine the exigencies posed to the nervous system, take place primarily on the body surface; therefore, the brain will increase interspecifically rather with the surface or the $\frac{2}{3}$ power of weight than with body weight itself. A similar idea was advanced by Quiring and Crile (Quiring, 1941), namely, that the brain regulates the heat output and increases, therefore, according to the exigencies of metabolism.

Thus, relative growth eventually leads to a "balance of the organs," to use the expression of classical morphology (Goethe, Geoffroy St. Hilaire), which is, in a crude way, intelligible by considerations like those given above.

This "balance of organs" necessary for the proper functioning of organisms belonging to a certain *bauplan*, and controlled by selection, has to be established in development. Thus, the final state to be reached is defined by the balance of the organs. However, the initial state will be different interspecifically since animals of different species are born in different states of maturity with respect to the various organs. To reach the prescribed balance of organs during the growth period, organs in different species must develop

with different speed, and this means that ontogenetic allometry will vary. Hence, the same end result (the balance of organs as defined by interspecific allometry) will be reached in different ways (ontogenetic allometry). This, then, is a case of equifinality as found in many biological processes. Equifinality is not a vitalistic feature, but is, in principle, derivable from the characteristic physical state of the organism, namely, its being an open system, developing towards a steady state (cf. Bertalanffy, 1950).

Such relation is clear with respect of the brain. Since the nerve cells do not multiply in postembryonic development, relative brain size is high at birth, and, since interspecifically proportionality only to the $\frac{2}{3}$ power of weight is demanded, ontogenetic allometry will be much more negative (ca. 0.2 intraspecifically for the rat, as compared to ca. 0.66 interspecifically for the series of mammals).

Summary

1) Allometric growth of some organs in the rat is described.

2) The relations between ontogenetic and evolutionary allometry (heterauxesis and allomorphosis) are discussed.

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PHYSIOLOGICAL EVIDENCE FOR NATURAL HYBRIDIZATION OF *BUFO AMERICANUS* AND *BUFO FOWLERI*

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Introduction

Members of the two toad species, *Bufo americanus* and *Bufo fowleri*,[2] apparently hybridize in areas where their ranges are in contact or overlap. Although naturalists have been aware of the existence of hybrids since the turn of the century, little intensive study of hybridization in nature has been undertaken until recent years. Hybridization was assumed by early workers (Miller and Chapin, 1910; Hubbs, 1918; Myers, 1927; Pickens, 1927; and others) largely from the presence of morphological intermediates in areas of intergradation. Blair (1941, 1942) confirmed earlier suggestions by demonstrating that laboratory crosses between *americanus* and *fowleri* give rise to viable hybrids, which resemble intermediate individuals collected in the field. The inference was reasonably made that the intermediate specimens found in nature owe their origin to interspecific crosses. Offspring of several experimental crosses were reared through metamorphosis, and male *fowleri-americanus* were backcrossed to female *americanus* and found fertile. Even though the hybrids were viable and apparently fertile, one cannot rule out the possibility that such hybrids are at a selective disadvantage to non-hybrids in nature. The relative survival value of the hybrids and non-hybrids can only be assessed by combining experimental investigations and field observations on alleged hybrid and parental populations.

Unless characters involving some aspect of viability or physiological efficiency are employed, little selective advantage can be attached to any of the morphological types encountered in the field. Studies by Moore (1949a, b and earlier papers) of various species of the genus *Rana* have indicated that a number of embryonic characters, such as rate of development and temperature tolerance, are closely correlated with geographical distribution of the species and represent adaptations on the part of each species to environmental temperature during breeding. These physiological characters are highly species-specific. In a series of experiments designed to reveal the adaptive nature of embryological characters in several species of toads, it has been demonstrated (Volpe, in preparation) that these characters are of value as a species-differential between *americanus* and *fowleri*. Consequently, these physiological characters would furnish a useful criterion of hybridization, as well as reveal any adaptive differences between the hybrid and putative parents.

With this view in mind, an investigation was undertaken along three lines. First, to explore the possibility of regional differentiation within each species, individuals from several populations of each species along the eastern coast were studied experimentally. This was necessary to avoid attributing an expression of geographical variation to hybridization. The second phase of the investigation involved laboratory crosses between the two species and observations on the rate of develop-

[1] This work was completed during tenure as a University Fellow (1951–1952), Columbia University, New York.

[2] Considerable confusion exists in the classification of toads. The two toad groups under consideration are classically treated as species. Recently, Netting and Goin (1946) have listed the American toad as *Bufo terrestris americanus*, and Fowler's toad is widely referred to as *Bufo woodhousi fowleri*.

ment of artificial hybrids. If artificial hybrid emybros have a modified rate of development, then one should reasonably expect to find deviations from the specific parental rates in natural hybrids. Third, the resulting data formed a framework for the interpretation of field studies and physiological analyses of a local population believed to be of hybrid origin.

If hybridization takes place, one would expect to find the strongest evidence for it in those regions where there is the greatest opportunity for hybridization. The local population investigated at West-

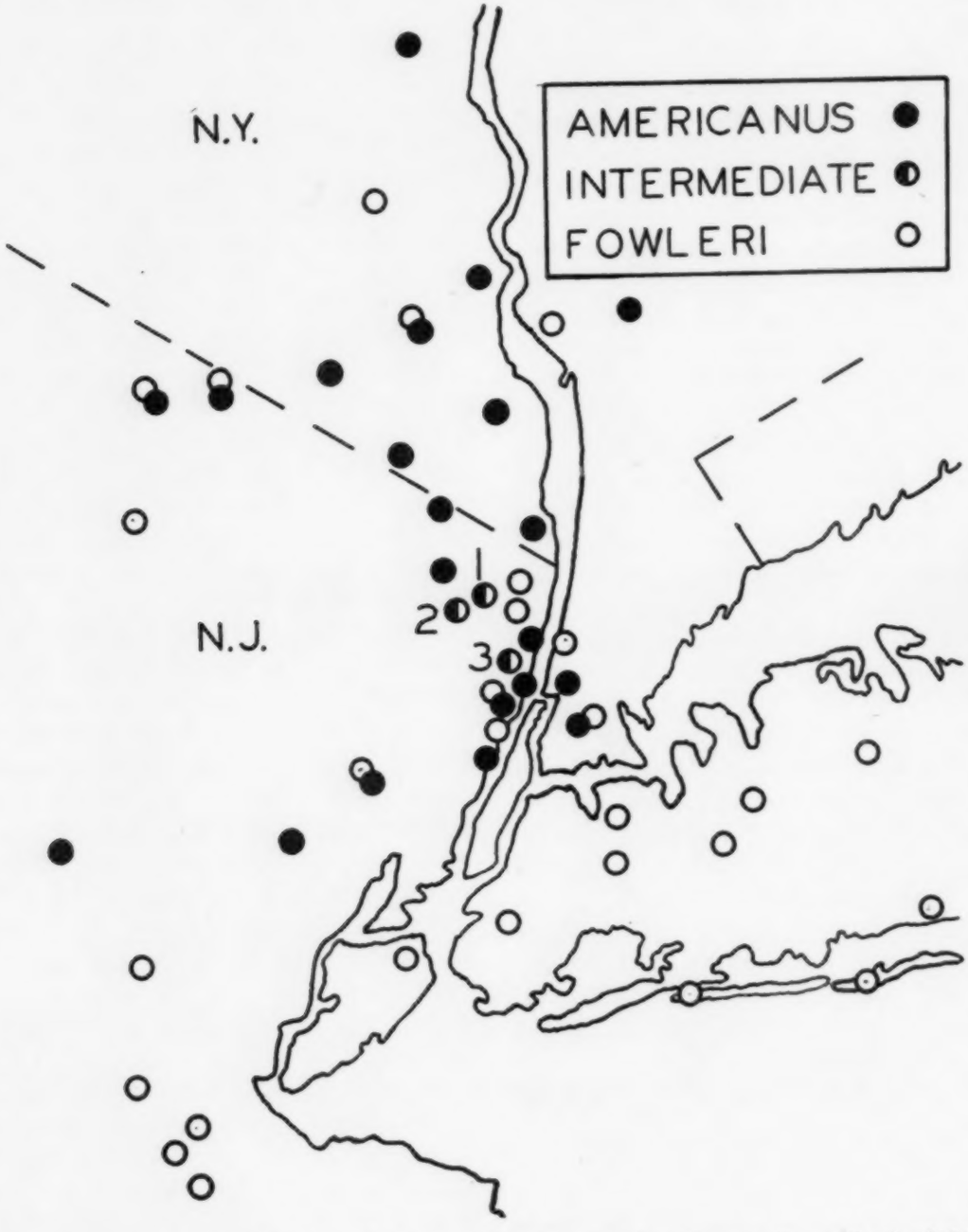

FIG. 1. Local distribution of toads. The data are based upon the author's field work and examination of specimens preserved at the American Museum of Natural History. The intermediate populations are represented by: (1) author's collection (Westwood, N. J.), (2) A. P. Blair's collection (Oradell, N. J.), and (3) J. A. Moore's collection (Tenafly, N. J.). Overlapping symbols signify that both species have been found at that particular locality.

wood, New Jersey, constitutes one of several areas in the northeastern part of the state where intermediate forms were anticipated from the regional distribution pattern of the two species (see fig. 1). Indeed, Blair (1947) has noted individuals that were assumed to be of hybrid derivation at Oradell, New Jersey; and Moore (1944) has suggested the occurrence of hybridization at Tenafly, New Jersey. The extensive hybridization suggested by field work at Westwood, New Jersey, has been supported by experimental analyses of adaptive temperature characteristics.

Field Observations

Since the morphological distinctions between the two species are imperfectly defined, the identification of a given individual rested upon consideration of the sum total of characters of that animal. The time of breeding and the mating call of the forms served to reinforce impressions derived from morphological examination. *Bufo americanus* is the characteristic form at higher altitudes, and at a given latitude, generally commences breeding two to six weeks earlier than *Bufo fowleri*. In the vicinity of New York City, *americanus* usually breeds during the early part of April and *fowleri* generally breeds during the middle of May.

A few observations relating to breeding habitats along the eastern coast are offered as a preliminary study concerning any differences in breeding sites of eastern representatives of the two species. They serve to indicate that a detailed ecological analysis is required before conclusions may be drawn as to the exact breeding habitat preferences of the two species. In the Adirondack Mountains, New York, the American toad breeds in the slow-moving tributaries of permanent lakes, which have mostly sand, gravel, boulder or natural rock beaches. At Equinunk, Pennsylvania, *americanus* tadpoles were collected in the sandy shallows of an eddy of the Delaware River; others were found in the shallow mudflats of the permanent Lake Bigelow at Wayne County, Pennsylvania. Mating pairs of *Bufo americanus* were also taken from temporary drainage ditches in the cultivated fields at New City, New York. Eastern *fowleri* likewise utilizes both permanent and temporary bodies of water. *Bufo fowleri* breeds in the temporary rain pools of the sand dune areas along the beach shores of southern Long Island, New York, and southeastern New Jersey, as well as in the shallows of permanent ponds in southern Long Island and northeastern New Jersey. At Winnsboro, South Carolina, actively calling *fowleri* were collected from temporary rain pools along roadsides and from washes in meadows. In many other areas, as well as in some of those mentioned above, man's extensive disturbance of natural conditions may have broadened ecological preferences of each species.

In the area of suspected hybridization, Westwood, New Jersey, the construction of the Oradell Reservoir in 1920 transformed a series of small creeks into a number of large shallow ponds. One of these permanent, quiet ponds has been studied by the writer for a period of two years.

1951 season:

In the spring of 1951, two large breeding congresses developed at the Westwood pond, on the evenings of April 28th, 29th, 30th and May 14th, 15th, 16th. On the evenings of April 28th and 29th, the morphological intermediacy of many of the members of the breeding chorus was apparent. These individuals varied among themselves, but they were not identifiable as either of the two species. The morphological divergence was not in many clearly definable independent characters, but could be best described as variously intermediate. Other individuals showed a greater influence of *fowleri* than of *americanus*. Members of this population were designated as Westwood "a."

This was the first sign of breeding activity in this pond, despite a diligent search prior to this time. The American toad populations at Bear Mountain, New York,

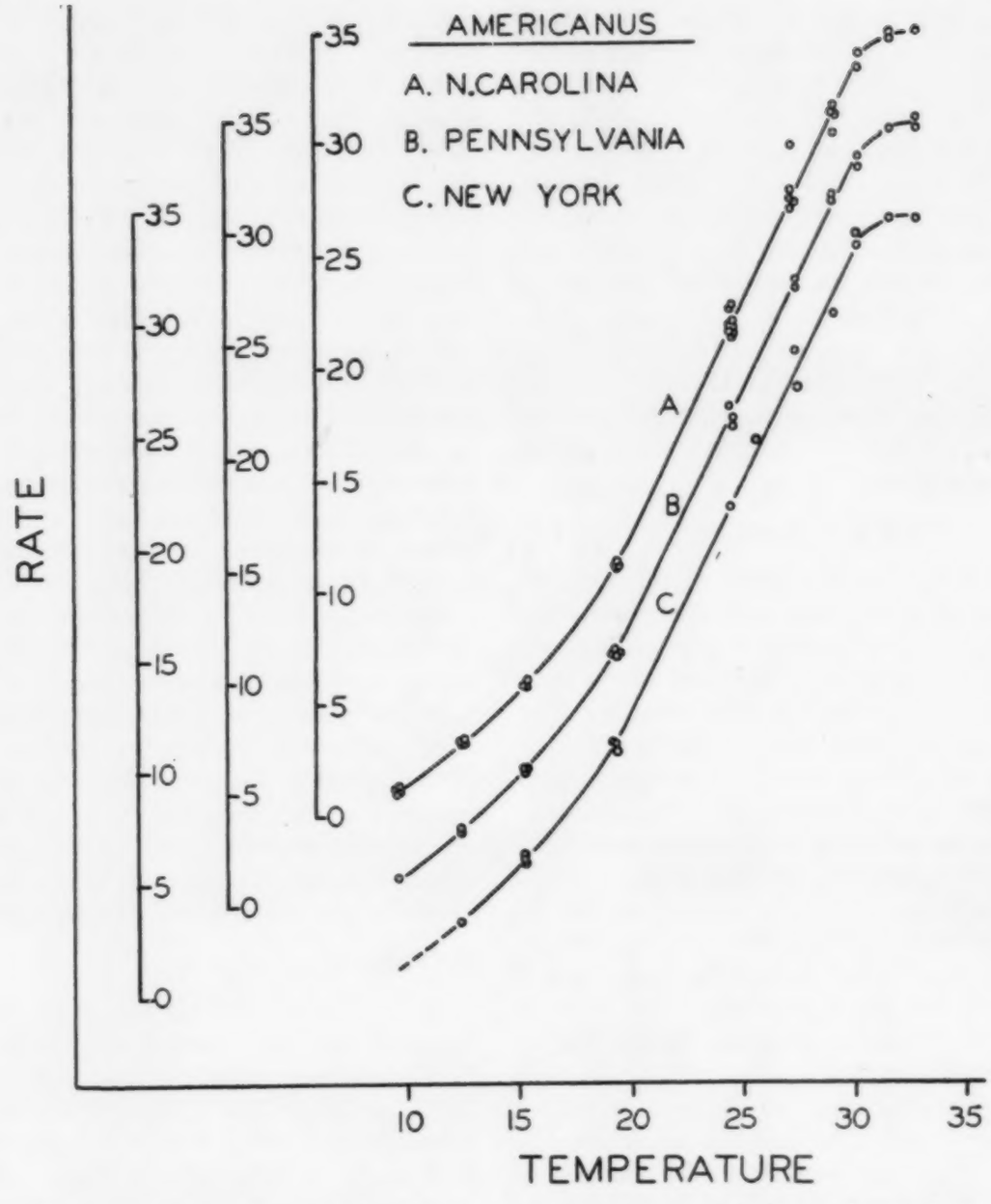

FIG. 2. A comparison of the rate of development of eggs of *Bufo americanus* from different localities. The ordinate represents the rate of development or 1,000 divided by the time, in hours, between stages 3 and 20; the abscissa, the temperature in ° Cent.

and vicinity had already bred, and Fowler's toad was not known to have emerged as yet. Numerous clutches of eggs were found the following evening, but after May 1st no further breeding activity could be detected in this pond, even after rains.

On May 15th, *fowleri* began its breeding activity in the New York region. Their mating calls were heard that evening on Staten Island and Long Island. A visit to the breeding site at Westwood revealed a large chorus of clearly recognizable *fowleri* individuals. Members of this population were designated as Westwood "b."

1952 season:

The spring of 1952 was unusually cold until the latter part of April, when marked rapid rises in temperature occurred. On the late date of April 18th, the American toad was found breeding in waters of

14° C. at New City, New York; and their calls were heard at Montvale, New Jersey. The spawning ground at Westwood was quiet that evening. On the exceptionally warm evenings of April 19th and 20th, large breeding congresses were observed at Westwood. The temperature of the pond water on these evenings measured 18° C. and 17° C. respectively. A marked heterogeneity was noticed in the breeding population; its members ranging from intermediate forms (presumably hybrids) to individuals closely resembling, if not being, pure *fowleri*. Individuals referable to what is generally considered "good" *americanus* were not found.

A revisit to the breeding site on April 22 revealed an unexpected phenomenon. The temperature of the pond water had dropped to 15° C. A few husky, droning notes of *fowleri* were heard, but these were overshadowed by a large chorus of peculiar "buzz saw" trills. The latter "hybrid" notes were the calls of structurally intermediate individuals. As far as could be detected, only more or less intermediate forms were breeding.

The 1952 Westwood array is referred to in the experiments as Westwood "c."

The field work at Westwood suggests that the emergence and breeding of the different morphological types is correlated with temperature conditions in the pond; *i.e.*, that even relatively small temperature differences result in a detectable shift in the composition of the population breeding at the time.

Experimental

A. Temperature adaptations in eastern americanus *and eastern* fowleri

The search for temperature adaptations were concerned with the embryonic stages, for it is during this period of the life of amphibians that the effects of temperature appear to be most marked. Complete de-

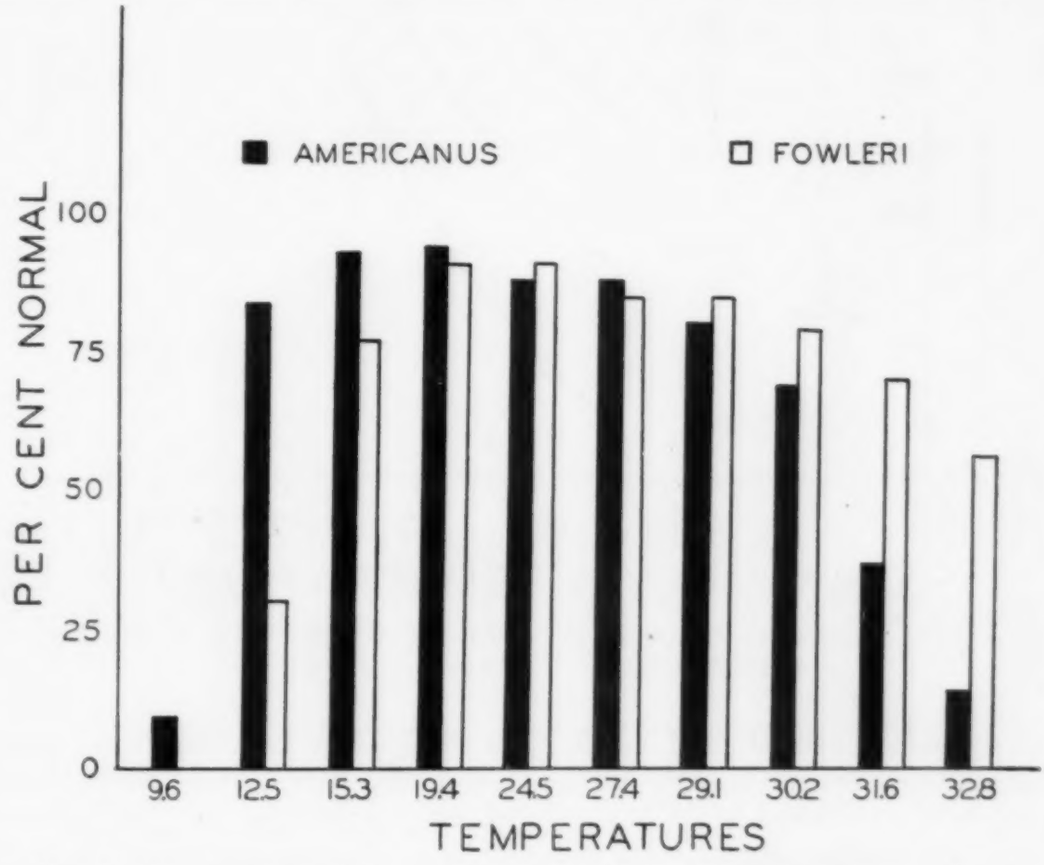

Fig. 3. A comparison of the average per cent normal development, at each temperature employed, of eastern embryos of the two species, *Bufo americanus* and *Bufo fowleri*.

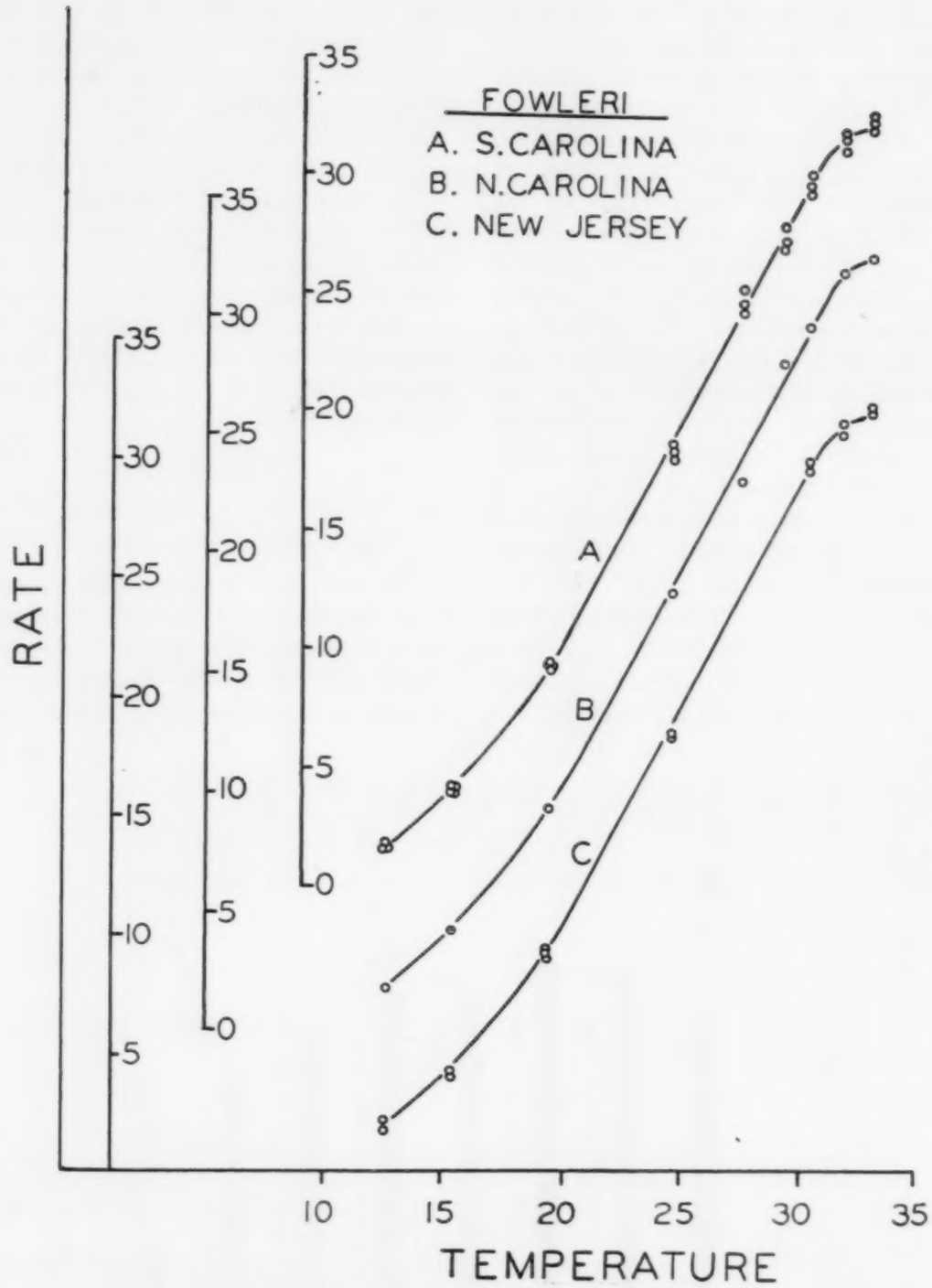

FIG. 4. A comparison of the rate of development of eggs of *Bufo fowleri* from different localities. Co-ordinates as in figure 2.

tails on methods of securing and handling fertilized eggs for temperature studies can be found in Moore (1949a).

Artificially fertilized eggs from a total of 15 mating pairs of *Bufo americanus* from the Adirondack Mountains, New York (Marcy Dam and Lake Colden); New City, New York; Delaware County, Pennsylvania; and North Carolina (Andrews, Franklin, and Rainbow Springs) were studied over a wide range of temperatures. No differences in rate of de-

velopment or temperature tolerance of *americanus* embryos from these localities could be detected.

Figure 2 shows the marked consistency in rate of development of embryos of these eastern *americanus*. The embryos are characterized by a rapid rate of development, particularly at low temperatures. The rate of development was determined by examining the embryos at each of the constant temperatures at regular intervals during development from first cleavage (stage 3) to a chosen end-point, gill circulation (stage 20). The stages of development are defined in Pollister and Moore (1937).

The proportion of survivals at the experimental temperatures (fig. 3) indicates that 31° C. and 10°–11° C. are the maximum and minimum limiting temperatures

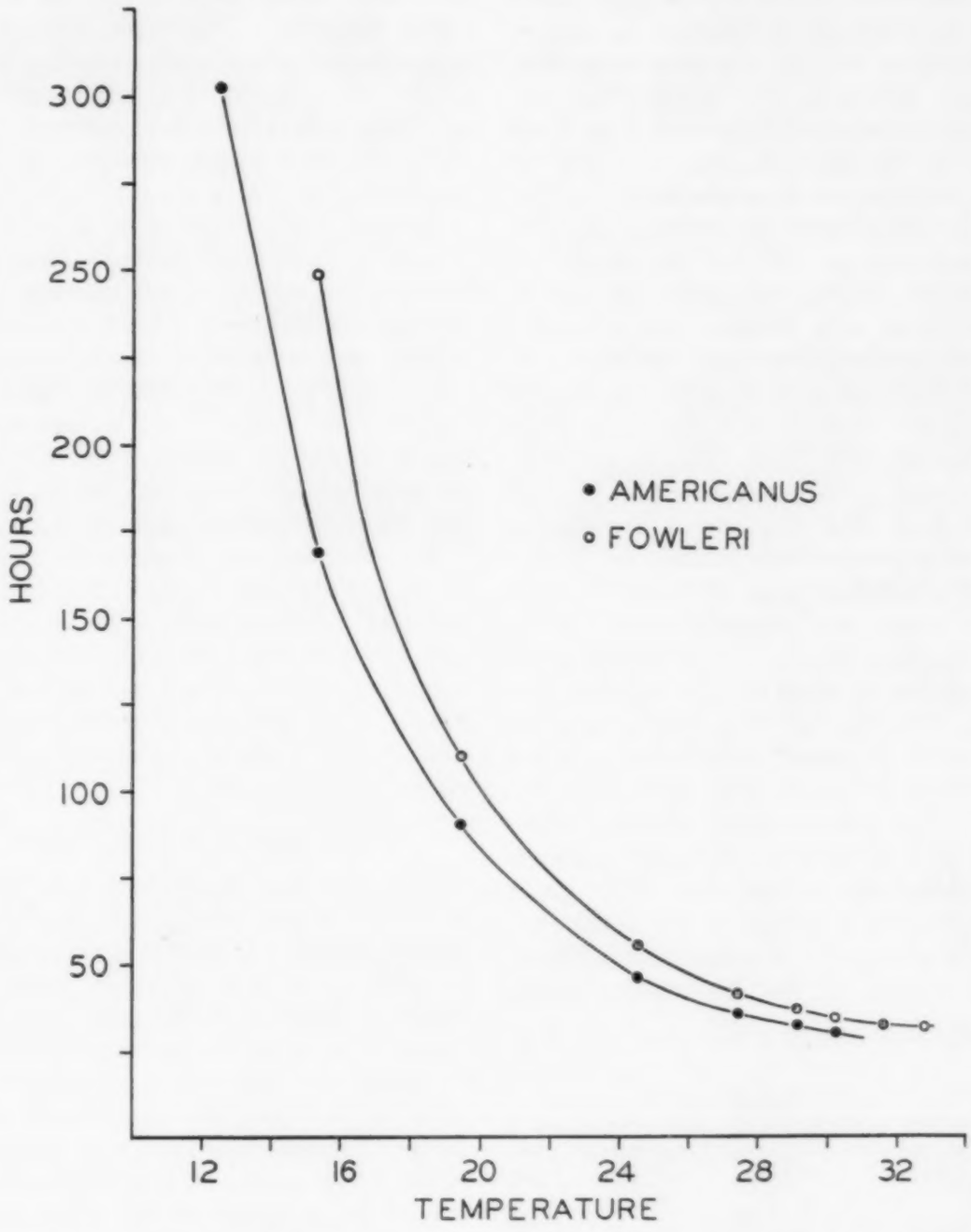

FIG. 5. A comparison of the mean time, in hours, between stages 3 and 20 at different temperatures, in degrees Centigrade, of eastern embryos of the two species, *Bufo americanus* and *Bufo fowleri*.

respectively for normal development.[3] Temperature tolerance was determined by the percentage of normal development observed over a range of temperature. A temperature at which less than 50% of normal development occurred was considered as a lethal temperature.

Experiments conducted on fertilized eggs of *Bufo fowleri* females from New Jersey (Westwood "b"); Sanford, North Carolina; and Winnsboro, South Carolina,[4] revealed no differences in rate of development (fig. 4) or embryonic temperature tolerance. The comparative survival of embryos of 9 females from these localities throughout the temperature range employed is shown in figure 3. The results indicate that the limits of temperature tolerance are 13°–14° C. and 33° C.

Marked differences in embryonic rate of development and temperature tolerance distinguish the two species. At each temperature tested, eggs of *Bufo americanus* reached the experimental end-point, stage 20, in less time than that required by embryos of *Bufo fowleri* (fig. 5). For example, at 19.4° C., eggs of *americanus* from New York, Pennsylvania, and North Carolina reached stage 20 in 89.9 ±0.24 hours (mean and standard error of the mean), as compared to 108.9 ±0.38 hours required by embryos of *fowleri* from New Jersey (Westwood "b"), North Carolina and South Carolina. The differences are even more pronounced at lower temperatures. The conspicuously greater differences at low temperature apparently reflect differential adaptations to the water temperatures in nature to which the eggs of each species are subjected. *Bufo fowleri* rarely breeds at the low environmental temperatures resorted to by *Bufo americanus*. At the experimental temperatures, 12.5° C. and 15.3° C., the time interval between first cleavage and gill circulation for eastern *americanus* embryos averaged 301.6 ±1.54 and 169 ±0.97 hours, respectively. Compared with eastern *fowleri* embryos (599.4 ±3.76 hours at 12.5° C.; 247.6 ±1.07 hours at 15.3° C.), this represents a developmental acceleration of 50% and 32%, respectively, for *americanus* embryos. The rapid rate of development of these early-breeding forms offsets what would be in other species a retarding effect on developmental processes of the low temperatures of their environment.

Eastern *americanus* embryos are able to tolerate lower temperatures than eastern *fowleri*, but are more susceptible to higher temperatures. This relationship is clearly seen in figure 3. In light of these results, the more restricted northern distribution of *fowleri*, and its absence at higher altitudes, suggest that embryonic temperature tolerance may be an important limiting distributional factor.

For the present investigation, our interest mainly centers upon the fact that regional differentiation, with respect to the physiological characters studied, is conspicuously lacking among eastern toads. Thus, any modification of developmental rate may be attributable to the effects of hybridization.

B. Artificial hybridization

In conducting the laboratory hybridizations, the method of artificial fertilization was employed. In order to eliminate any possible variability caused by individual heredity differences, the eggs of a single female were used for both the hybrid and "normal" crosses. The procedure consisted of fertilizing the eggs of one female in two batches; the first with the sperm of the same species ("normal"), the second with the sperm of the other species. Simultaneous observations were made of the embryonic rate of development of the experimental hybrids and normals at vari-

[3] A detailed account of the embryological aspects of the influence of temperature on development will be published elsewhere.

[4] Practical considerations have prevented a study of pure *fowleri* from Long Island, New York. However, Moore's brief note (1944) on rate of development of *fowleri* eggs from Flushing, L. I. reports a time interval of 107 hours between first cleavage and gill circulation at 19.3° C. This agrees well with my results on eastern *fowleri*.

ous temperatures. The following crosses involving eastern forms were performed:

(a) *fowleri*, South Carolina ♀ × *fowleri*, South Carolina ♂
× *americanus*, North Carolina ♂

(b) *fowleri*, North Carolina ♀ × *fowleri*, North Carolina ♂
× *americanus*, North Carolina ♂

$(c)_1$ *americanus*, Pennsylvania ♀ × *americanus*, Pennsylvania ♂
× *fowleri*, South Carolina ♂

$(c)_2$ *americanus*, Pennsylvania ♀ × *americanus*, Pennsylvania ♂
× *fowleri*, South Carolina ♂

In all these crosses, the results on hybrid rate of development were consistent. No developmental irregularities were found. At 19.4° C., the embryonic development of the reciprocal hybrids proceeded synchronously with the rate of the maternal species until late gastrulation. At the close of the neural plate stage, a reverse developmental deviation of the reciprocal hybrids from the maternal rates occurred, which continued through later stages (table 1). The final effect was that the *americanus* ♀ × *fowleri* ♂ hybrids developed slightly more slowly than the *americanus* normals, whereas the hybrids of *fowleri* ♀ × *americanus* ♂ developed slightly faster than the *fowleri* normals. Experiments at other temperatures gave similar results.

Temperature tolerance values show

TABLE 1. *Stages in the development of Pennsylvania* Bufo americanus *and South Carolina* Bufo fowleri *normals, and hybrids of Pennsylvania* Bufo americanus ♀ × *South Carolina* Bufo fowleri ♂ *and South Carolina* B. fowleri ♀ × *North Carolina* B. americanus ♂

An "=" sign between two figures indicates that the embryos being compared are indistinguishable in developmental stage attained. A ">" sign indicates that the embryos in the left column are more advanced. A "<" sign indicates that the embryos in the left column are less advanced. Experiment conducted at 19.4° C.

Age (hours)	Stages: Pa. *amer.* ♀ × Pa. *amer.* ♂		Stages: Pa. *amer.* ♀ × S. C. *fowleri* ♂	Age (hours)	Stages: S. C. *fowleri* ♀ × S. C. *fowleri* ♂		Stages: S. C. *fowleri* ♀ × N. C. *amer.* ♂
0	3		3	0	3		3
3.5	5	=	5	8.2	7	=	7
13.2	9	=	9	11.2	8	=	8
16	10e	=	10e	14	9	=	9
18.5	11e	=	11e	18.5	10e	=	10e
21.7	12e	=	12e	21.5	11e	=	11e
25	12m	=	12m	32.7	13e	=	13e
27.5	12L	=	12L	37.5	14e	<	14m
37	13L	=	13L	41.5	14m	<	14L
39	14e	>	13L	44.5	14L	<	15
41.7	14m	>	14e	46.5	16m	<	16L
44.7	16e	>	14L	56.2	17e	<	17m
48	16m	>	16e	59.2	17	<	17
51.7	17e	>	16L	62.2	17	<	17
62	17m	>	17e	65.7	17	<	17L
69	18e	>	17L	68.5	18e	<	18m
71.7	18m	>	18e	80.2	18	<	18
76.5	19e	>	18L	82.5	18m	<	18L
86	19m	>	19e	87.5	18L	<	19e
90	20e	>	19m–L	90.5	19e	<	19m
93.7	—		20e	94.5	19e–m	<	19m–L
				102.5	19m–L	<	19L
				105.5	19L	<	20e
				109.0	20e		—

clearly a maternal influence. Cross (a) was maintained at 19.4°, 30.2°, 31.6° and 32.8°; Cross (b) was maintained at 19.4°, 24.6° and 9.6°. Gastrulation was impeded in both the normals and hybrids at 9.6°; at the higher temperatures, fairly good development typical of *fowleri* eggs was observed. Cross $(c)_1$ was maintained at 19.4°, 30.2°, 31.6° and 32.8°; Cross $(c)_2$ at 19.5°, 24.5°, and 15.3°. At temperatures above 30°, the hybrids fared no better than the *americanus* normals.

Thus, it is seen that the reciprocal hybrid rates of development and temperature tolerance are not intermediate, but are more or less like the respective maternal forms. In this way, loss of these hybrid embryos through unfitness to existing conditions is avoided. It seems fair to presume that in nature each society is capable of supporting the progeny resulting from reciprocal crosses.

C. The Westwood population

The experimental results of the two years' collection at Westwood are considered separately.

The development of six groups of Westwood "a" embryos was studied. Data on temperature tolerance and rate of development are compared to the data of eastern *americanus* and eastern *fowleri*. Embryos of three Westwood "a" females were raised at the wide span of temperatures normally employed; eggs of three other females were maintained only at 19.4°. At 9.6°, all three groups of embryos developed as far as the tail-bud stage, and

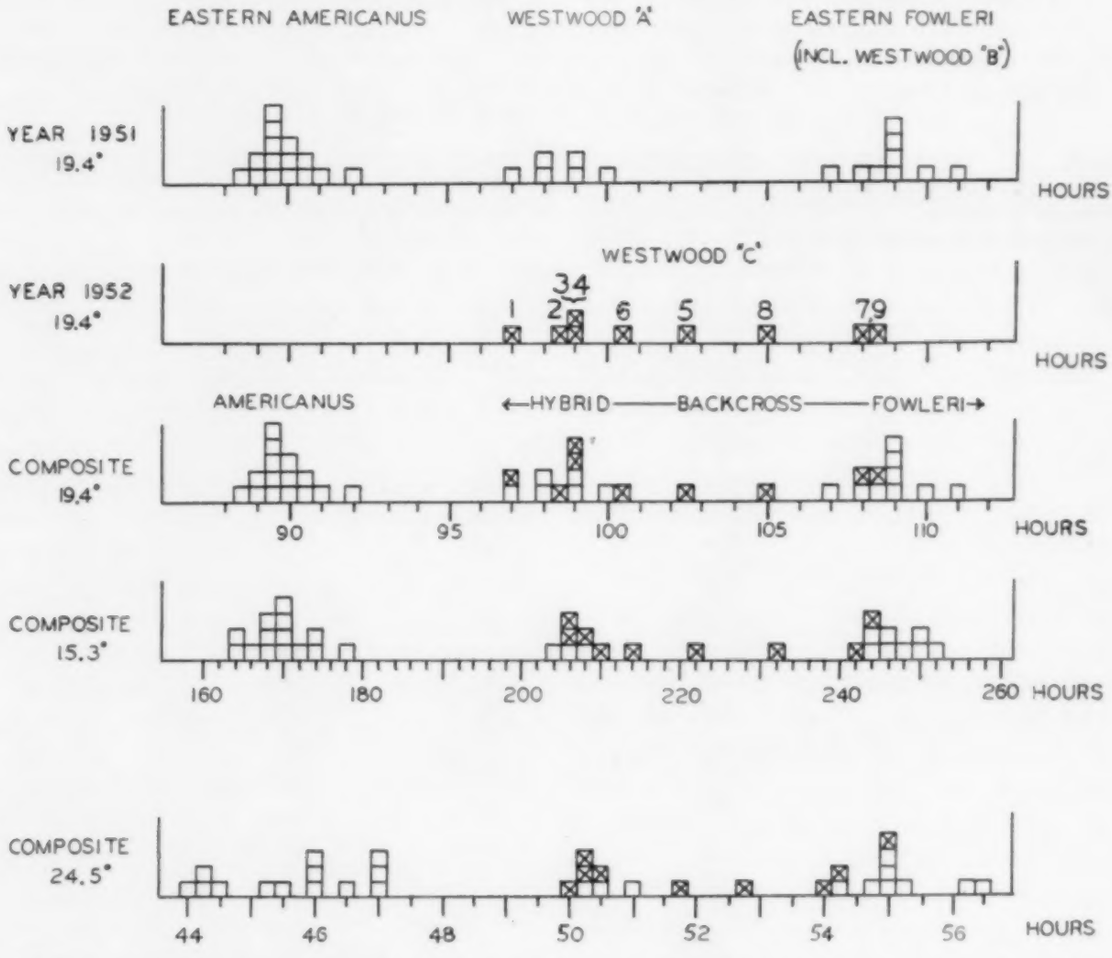

FIG. 6. A summary and comparison of the development of fertilized eggs of mating pairs of eastern *americanus*, eastern *fowleri*, and the two years' Westwood population at three temperatures, 19.4°, 15.3° and 24.5°. Each square represents the time, in hours, between stages 3 and 20 of a cluster of fertilized eggs of a single female. For other explanation, see text.

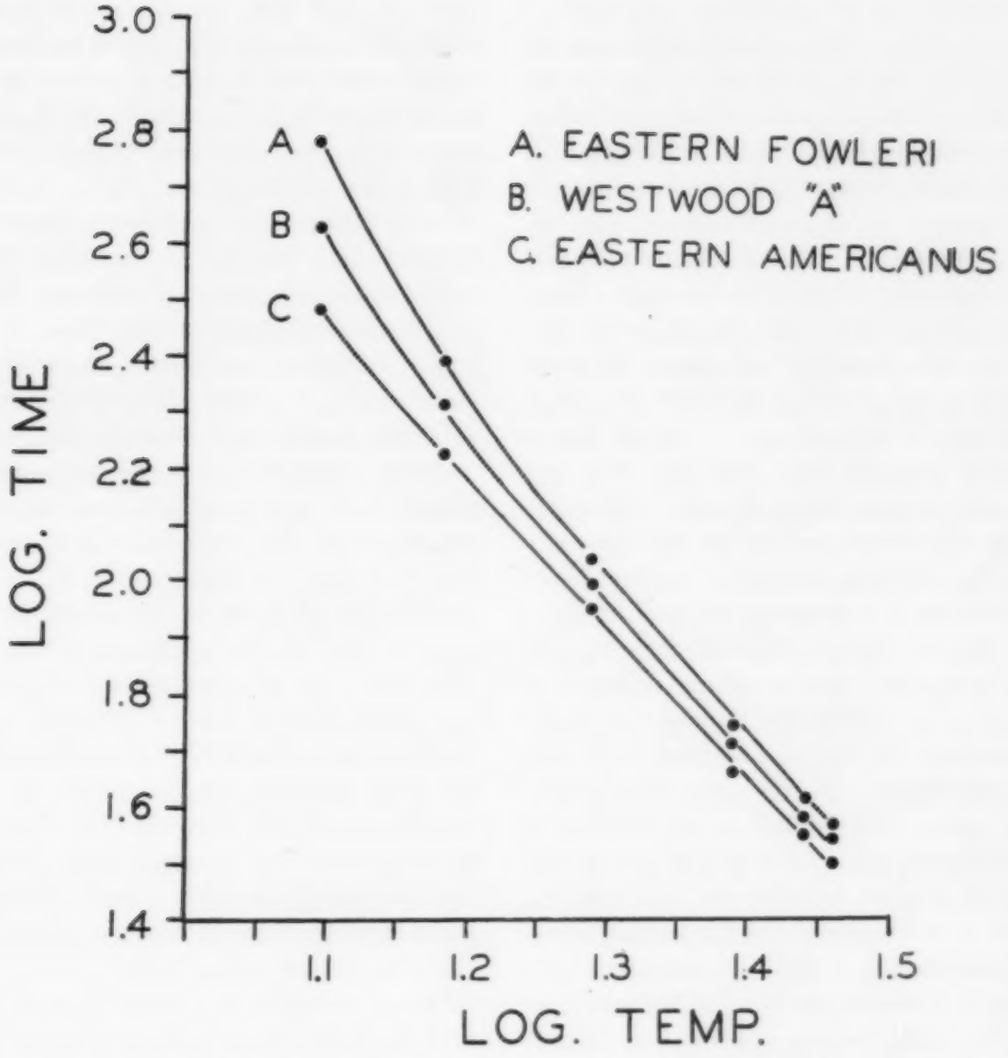

FIG. 7. A log. time- log. temperature plot of the mean time, in hours, between stages 3 and 20 at different temperatures, in degrees Centigrade, of embryos of eastern *americanus*, the Westwood "a" population, and of eastern *fowleri*.

died. Eastern *americanus* eggs at this temperature developed past the tail-bud stage, whereas eastern *fowleri* eggs at 9.6° failed to survive beyond gastrulation. At 12.5°, development was normal which compares well with the reaction of *americanus* eggs at this temperature. The embryos did not show the low temperature defects exhibited by *fowleri* eggs at 12.5°. At 19.4°, 24.5°, 29.1° and 30.2°, development was normal. At 31.6°, a temperature found to be generally fatal to *americanus* eggs, the Westwood "a" embryos were better adapted. Thus, the embryos of the more or less intermediate individuals appear to combine the embryonic temperature tolerance characteristics of each species.

The most interesting feature of the Westwood "a" embryos was their intermediate rate of development. At 19.4°, a temperature chosen for the accumulation of the most data, the time interval between first cleavage and gill circulation averaged 98.5 ±0.43 hours (mean and standard error of mean). At this same temperature, eggs of eastern *americanus* reached stage 20 in 89.9 ±0.24 hours, whereas eastern *fowleri* embryos required 108.9 ±0.38 hours. The differences are significant. This relationship is represented in histogram form (fig. 6, top column), which shows that the rates of development of Westwood "a" embryos at 19.4° are quite distinctive, and do not fall

within the range of variability of either of the two species. The intermediate rate of development throughout the temperature range employed is readily apparent when the data are plotted on a log. scale (fig. 7).

The results of the 1952 experiments are best presented in histogram form (fig. 6, second column), which permits ready comparison with the 1951 results. Very striking gradations were observed in the rates of development of the different groups of fertilized eggs derived from nine Westwood "c" females. We find types with the intermediate rate of development, progressing toward, and including, the slow rate characteristic of pure *fowleri*. The different experimental mating pairs were arranged according to visible characters from hybrid tendencies to "pure" *fowleri* (nos. 1–9 in the second column of fig. 6). The difficulty of distinguishing between individuals of partial hybrid ancestry and those of the uncontaminated *fowleri* stock is reflected in the disturbed order toward the *fowleri* range of the scale. It is also of considerable interest to note that the rates of development of two clusters of eggs derived from two mating pairs captured on the cool evening of April 22, 1952, when only more or less intermediate forms were breeding, are represented by nos. 1 and 3.

Analyzing the composites for the two years' results at 19.4°, 15.3°, and 24.5° (fig. 6), the Westwood population is characterized by morphological intermediates (hybrids), whose embryos possess an intermediate rate of development; *fowleri* individuals, with embryonic temperature characteristics like those of pure *fowleri* found in other localities; and experimentally detected backcross individuals.

Discussion

There seems to be no interspecific sterility between *Bufo americanus* and *Bufo fowleri*. Apparently, the gene complexes determining the rates of physiological processes in each species are interchangeable without detrimental effects in the progeny. Such a situation may be advantageous, for new adaptive peaks may be realized from hybrid combinations. In areas where the ranges of *americanus* and *fowleri* overlap, intrinsic isolating mechanisms have not developed, and there is no reason to suppose that such barriers to hybridization will appear. Dobzhansky (1941) has proposed that reproductive isolating mechanisms develop through natural selection against the loss of fitness which occurs when two species hybridize. Conversely, it seems plausible that natural selection would not promote the establishment of reproductive isolating mechanisms if no loss of fitness results from intercrossing between two species. As far as one can tell, the viability and fertility of the experimental hybrids of *americanus* and *fowleri* are normal (Blair, 1941, 1942). The present investigation indicates that morphologically and physiologically intermediate individuals, considered to be hybrids, are able to survive in nature.

The possibility that the observed intermediates from Westwood, New Jersey, are chance recombination products of *Bufo fowleri* is unlikely as one would not expect such large numbers of extreme variants. They probably do not represent geographical variants, since experimentation has shown that regional differentiation in the physiological characters studied is lacking among eastern representatives of the two species. They may represent *americanus* individuals which have converged toward *fowleri* characteristics through parallel selection of similar genes. For the present, at least, this unworkable hypothesis may be discounted. All the available information on the geographical distribution, habitat selection, and breeding behavior of the parental species is quite in harmony with the view of hybridization.

Individuals from Westwood range from intermediates (hybrids) to pure *fowleri*, and are distinguishable from one another by the response of their embryos to temperature. The experimental data suggest that the population as a whole consists predominantly of intermediates and pure *fowleri*, with a limited number of back-

cross individuals occupying a trough between the two apparent peaks. This may not be the actual case. Prior to experimentation, the developmental rates of embryos of morphologically diagnosed hybrids and morphologically diagnosed *fowleri* could be predicted with a fair degree of accuracy. However, the experimentally detected backcross individuals could not be determined beforehand by the writer on a purely morphological basis. In other words, the lack of a greater number of experimental cases of individuals of backcross origin may be a sampling error based on uncertainty of morphological recognition of such forms. More extensive physiological data would be necessary to characterize the population with more assurance in terms of relative frequency of different types.

It is generally acknowledged that physiological differences between species segregate in the same manner as morphological ones. If this pertains to the initiation of breeding in toads, then one result of hybridization would be the formation of a variety of individuals, each of which would require its own peculiar set of conditions for breeding. At Westwood, recognizable intermediate individuals appear to emerge earlier and breed at lower water temperatures than recognizable *fowleri* individuals. The different requirements for breeding of hybrid adults may be causally associated with the different temperature adaptations of the hybrid embryos. It may be inferred that the intermediates resemble *fowleri* sufficiently in their ecological requirements to survive and compete with them, as well as possess certain ecological advantages which enable them to maintain themselves as such in considerable numbers. Whether sufficient selection pressure has been exerted on the early-breeding hybrids so that they would not be considered as part of the *fowleri* breeding community must await the accumulation of considerably more data than are now available.

The maintenance of recognizable, early-breeding intermediates depends upon the extent of backcrossing to *fowleri*. Extensive gene flow can neutralize the effects of different selection pressure in the hybrid and later-breeding *fowleri* individuals. Intensification of preferential matings could, however, mitigate the swamping effects of gene flow.

The net result of continual backcrossing or introgression would be one of imparting greater variability to the *fowleri* group. Such a situation is, in a sense, a negative one for evolutionary processes since the adaptive fitness of the specialized *fowleri* stock would be decreased. Yet, the resultant increase of potential variability through introgression "buffers" the species against changing environments.

Two years of collecting at Westwood have failed to reveal the presence of individuals with predominantly *americanus* characteristics. However, the American toad has been reported from Westwood. A "good" *americanus* specimen dating back to May 3, 1930, and marked "Westwood, N. J." appears in the collection at the American Museum of Natural History (AMNH A36740).

Irrespective of which species originally inhabited the area, the presence today of *fowleri* to the exclusion of *americanus* indicates that the former is better adapted to prevailing conditions. Considering the above point, certain conjectures relating to the absence of *americanus* at the Westwood pond may be permitted. In the segregative hybrid population which arose when one species invaded and hybridized with the other, it may be supposed that only those individuals most nearly resembling *fowleri* in ecologically important characters proved superior and were selected. In competition with the great variety of hybrids containing adaptively valuable *fowleri* alleles, the original invading or formerly established *americanus* population was displaced. It is also conceivable that the *americanus* characteristics have been largely "absorbed" by extensive back-crossing to the more abundant *fowleri* individuals. As another alternative, it may be proposed that the

americanus population has migrated. If the emigrants have spread out elsewhere, then one may possibly perceive a "cline of hybridization." In other words, *americanus* individuals in closely adjacent areas may show *fowleri* influences, although the visible effects may be so slight as to escape detection.

It is hoped that future investigations will shed some light on these and other possibilities.

Summary

Field observations of the apparently successful establishment of hybrids of *Bufo americanus* and *Bufo fowleri* at Westwood, New Jersey, have been confirmed by experimental analyses.

Two physiological characters, embryonic rate of development and embryonic temperature tolerance, have been demonstrated to provide a uniform and constant differential between the two toad species. The usefulness of these adaptive embryological characteristics as a criterion of hybridization is attested by the fact that embryos of presumed natural hybrids exhibit an intermediate rate of development.

The hybrids at Westwood differ among themselves, some of them being clearly intermediate between the two species, others resembling *fowleri* more than *americanus*. *Bufo fowleri* is found in abundance at this particular locality, but individuals with predominantly *americanus* characteristics are apparently lacking. Prior to experimentation, the obvious intermediates and the recognizable *fowleri* could be predicted to have characteristic rates of development. Backcross individuals are difficult to distinguish morphologically, but their hybrid ancestry can be detected by the departure of their embryonic rates of development from the group averages.

Acknowledgments

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COMPETITION BETWEEN *DROSOPHILA MELANOGASTER* AND *DROSOPHILA SIMULANS*. I. POPULATION CAGE EXPERIMENTS

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INTRODUCTION

Drosophila melanogaster and *Drosophila simulans* are sibling species that were not distinguished from each other until Sturtevant described the latter in 1919. Their remarkable morphological similarity is well known to Drosophila geneticists. As a measure of their near identity it might be mentioned that several investigators experimented with strains of both species simultaneously and were unaware that they were not dealing exclusively with *melanogaster*.

According to Sturtevant (1920), it was C. B. Bridges who first noticed the peculiar male genitalia of *simulans*. This feature allows easy separation of the males of the two species but there is no reliable and rapid means of distinguishing females.

The close similarity of *melanogaster* and *simulans* is not restricted to externals. There is a corresponding parallel in genetics (Sturtevant, 1920, 1921a, 1921b, 1929; and Sturtevant and Plunkett, 1926). Both species have four linkage groups and many of the mutations that have arisen in *simulans* are allelomorphs of those in *melanogaster*.

Comparisons of the salivary gland chromosomes were made by Pätau (1935), Kerkis (1936, 1937) and Horton (1939). A study of the hybrids showed a striking similarity of the salivary chromosome bands of the two species. There is one large inversion in the third chromosome which previously had been detected genetically by Sturtevant. In addition there are 5 very short inversions, 4 instances where the bands differ at the free ends of the chromosomes, and 14 regions where the chromosomes do not synapse in spite of the fact that the chromosomes appear to be identical.

Hybridization is difficult. Sturtevant (1929) reported that offspring are obtained in from 10 to 40 per cent of the *melanogaster* ♀ × *simulans* ♂ crosses and in not over 2 per cent of the *simulans* ♀ × *melanogaster* ♂ crosses. The first cross produces females and a few exceptional males. The second produces many males and a few females. All hybrids are sterile. So far as mating preference is concerned, Sturtevant found that males will court females of the opposite species but females prefer to mate with members of their own kind.

When Sturtevant published his monograph on *simulans* in 1929, all geographical records known to him were from the western hemisphere. Subsequently, *simulans* has been recorded from Europe, Australia and Asia (Kikkawa and Peng, 1938). It is probable that *melanogaster* and *simulans* are widely distributed in tropical and temperate zones throughout the world. In most regions they are commonly associated with human habitations and natural areas contiguous with human habitations.

Some ecological differences between *simulans* and *melanogaster*, which may be of importance in competition under natural conditions, have been noted by several authors. Patterson (1943) studied an area near Austin, Texas, where both species occur. *Simulans* is more abundant in the late autumn months. During the coldest period of the winter the population size of both species is greatly reduced. With the subsequent temperature increases the

melanogaster population builds up rapidly while *simulans* remains rare. During the hot dry months the *melanogaster* population suffers a marked decline and *simulans* increases to become the more abundant. Its preponderance lasts until the winter reduction in populations size. Burla (1948) speaks of *simulans* as being a more southern species, compared to *melanogaster*. Dobzhansky and Pavan (1950) report that *simulans* is more abundant than *melanogaster* in Brazil.

With respect to rate of development Sturtevant (1929) found that ". . . the two species are very nearly the same; but comparisons (made under rather loosely controlled conditions) have several times suggested that *simulans* develops slightly more rapidly." Regarding food habits he states, "Casual field and laboratory observations suggest differences in food preference, since *simulans* is rarely found on apples, is relatively commoner on bananas, and seems to be still more frequent on persimmons." Morgan (1929) remarks on the fact that *simulans* females are sometimes fertilized a few hours after emerging, implying a shorter period than is possible for *melanogaster*.

Spieth and Hsu (1950) have reported slight differences in courtship pattern of the two species. In addition, they report that *melanogaster* females are inseminated equally well in both light and dark, but *simulans* females are inseminated much more frequently in light than in the dark.

The general conclusion that one draws from published work on *simulans* and *melanogaster* is that the species are strikingly similar. This applies not only to external appearance but to genetics, chromosome morphology, geographic distribution, and habitat preferences. In situations of this sort the question inevitably arises, "how do the two forms coexist in nature?". Since Darwin's time it has been appreciated that intensity of competition is directly proportional to degree of similarity. In this case, therefore, competition must be intense. There is, however, another factor to consider. With any two sibling species, it seems probable that similarity in physiology and ecology can never be carried to the point of identity. Instead, differences must exist that tend to reduce competition between species enough to allow coexistance. At the moment this is more an article of faith than fact but it seems most probable that this is a correct point of view.

This paper will be devoted to a study of competition between *Drosophila melanogaster* and *Drosophila simulans*. It will be concerned with the outcome of competition in "population cages," differences between the two species that are of importance in competition, and attempts to influence the course of competition by modifying the conditions of the experiments.

These are not the first experiments on competition between *simulans* and *melanogaster*. Sturtevant (1920) reported that both species could be kept in mixed stocks, using the ordinary laboratory technique, for as long as five months. *Melanogaster* was the more abundant species until the food became old and dry. Under the latter conditions *simulans* increases in frequency. Sturtevant speculated that "Greater resistance to such unfavorable conditions may perhaps account for the fact that *simulans* maintains itself in nature in spite of the fact that, under favorable conditions, it is outdone by *melanogaster*."

Materials and Methods

Two *simulans* strains, numbers 75 and 76, which were collected at Bradenton, Florida, in January 1949, and three strains of *melanogaster*, numbers 92, 97, and 99, collected at the same locality in February 1949, were used in the experiments. In most of the experiments only *simulans* 75 and *melanogaster* 99 were used. I am indebted to Dr. H. Spieth for all of these. These wild strains were derived from single fertilized females. In the early experiments the stocks were mass cultured in bottles. Somewhat later stock cages of *simulans* 75 and *melanogaster* 99 served as sources of the material.

The population cages employed in the experiments were designed by Wallace and are somewhat similar to those described by him in 1949. They are constructed of plastic and the outside dimensions in centimeters are 46 by 13 by 11. At one end of the cage there is a wire mesh opening 74 cm.^{2} The internal space for the flies is approximately 5,000 cm.^{3} The bottom of the cage contains holes for 16 food cups. The latter have a capacity of 30 cc. each. The exposed food surface of each cup is 4.5 cm.^{2}

The food was Spassky's (1943) cream of wheat-molasses mixture enriched with brewer's yeast and with "tegosept" substituted for "moldex." A drop of brewer's yeast was placed on the surface of each cup before it was used.

The population cages were kept in constant temperature rooms, one at 15° and the other at 25°. Both rooms were dark much of the time. Humidity was not accurately controlled. These same rooms were used by Levitan (1951). He found a variation in the mean monthly relative humidity of from 62.7 ±0.8 to 83.5 ±0.9 for the 15° room and from 65.8 ±0.4 to 76.5 ±0.7 for the 25° room. It is probable that the variations were similar during the course of my experiments. The humidity within the cages is probably somewhat higher than that recorded in the constant temperature rooms.

The sequence of events in cups in the 25° experiments may be outlined as follows. Eggs begin to be deposited in a few minutes after the cups are placed in the cages. In 2–3 hours the number may be several hundred and after 1 day the number may be in the thousands. The average number of adults that arise from each cup during a single generation is approximately 500.

Larvae begin appearing in less than a day and pupae in less than a week. The first adults emerge on the eighth or ninth day. These cups may give rise to later generations. In most cases mold growth was slight, especially when cups were changed at the standard rate of 4 per week in the 25° experiments.

Changes in the relative numbers of these two species were measured by periodic egg samples. The procedure was as follows. A cup would be placed in the cage and left for 1 day in the 25° experiments or for 2 days in the 15° experiments. It would then be removed from the cage and 4 small pieces of the surface food containing eggs would be cut out. These were placed in 4 half pint fly bottles (with food). An attempt was made to regulate the number of embyros developing in each bottle so that not more than several hundred would be present. In this way competition was greatly reduced and the egg sample is essentially a measure of the relative numbers of viable eggs deposited. When the adults emerged the males were classified and counted. This indirect way of measuring population changes was thought to be more desirable than etherizing and counting the entire adult population. Several counts indicated a fairly close relation between relative frequencies of the adults in the cage and relative frequencies of viable eggs deposited.

During the course of the experiments it was found that the oviposition sites of the two species are not identical. When this was realized the procedure was modified and two samples were taken from the center area of the food cup and two from the edge. This change in procedure was not reflected in the data so it is assumed that the original method of taking 4 samples at random was leading to essentially the same result.

All developing egg samples were kept at 25° irrespective of the temperature at which the population was being kept.

During the course of the experiments the cages would become dirty from the accumulation of dead flies and the occasional overflowing of the food cups. When this occurred the cups and adults were transferred to a clean cage. In general, the 25° cages were changed every 4–6 weeks.

A. Competition Experiments at 15° and 25°

The following experiment will serve to introduce the data on competition between *melanogaster* and *simulans*. A total of 600 *melanogaster* females (150 each from stocks 92, 97, 99 and another 150 derived from a wild type fly caught in the laboratory) and 300 *simulans* females (150 each from stocks 75 and 76) were placed in a cage with 16 cups. These females were allowed to oviposit for two days and then the food cups were removed. These cups were placed in an empty cage to start cage 2. This procedure was repeated three times and the cups secured were used to start cages 3, 4, and 5. The populations of cages 2, 3, 4, and 5, therefore, were started from the same adult population.

Cages 2 and 4 were kept at 25° and when the adults began to appear the cups were changed at the rate of 4 a week (Tuesday 1, Thursday 1, and Saturday 2).

Cages 3 and 5 were kept at 15.5° and when the adults began to appear the cups were changed at the rate of 2 a week (Tuesday 1, Saturday 1).

Egg samples were taken at the start of the experiment and at intervals thereafter. The initial samples are measures of the relative numbers of eggs being laid by the two species and not of competition.

The 25° experiments. Cages 2 and 4 gave essentially the same result. The data for these and subsequent experiments will be given as follows: number of days from start of experiment—per cent *melanogaster* males, (total *simulans* and *melanogaster* males).

Cage 2: 1 day—77 per cent *mel.* (426); 21 days—51 per cent *mel.* (299); 42 days—82 per cent *mel.* (514); 51 days—97 per cent *mel.* (208); 62 days—99 per cent *mel.* (274); 80 days—100 per cent *mel.* (122).

Cage 4: 1 day—52 per cent *mel.* (199); 22 days—53 per cent *mel.* (538); 47 days—99.5 per cent *mel.* (200); 62 days—100 per cent *mel.* (140); 76 days—100 per cent *mel.* (151).

These data are shown graphically in figure 1. The rapid elimination of *simulans* by *melanogaster* is the usual result of experiments conducted at 25°.

The 15° experiments. Competition between *melanogaster* and *simulans* at 15° leads to a result different from that found at 25°. See also figure 2.

Cage 3: 1 day—38 per cent *mel.* (208); 52 days—52 per cent *mel.* (93); 106 days—37 per cent *mel.* (614); 154 days—19 per cent *mel.* (498); 200

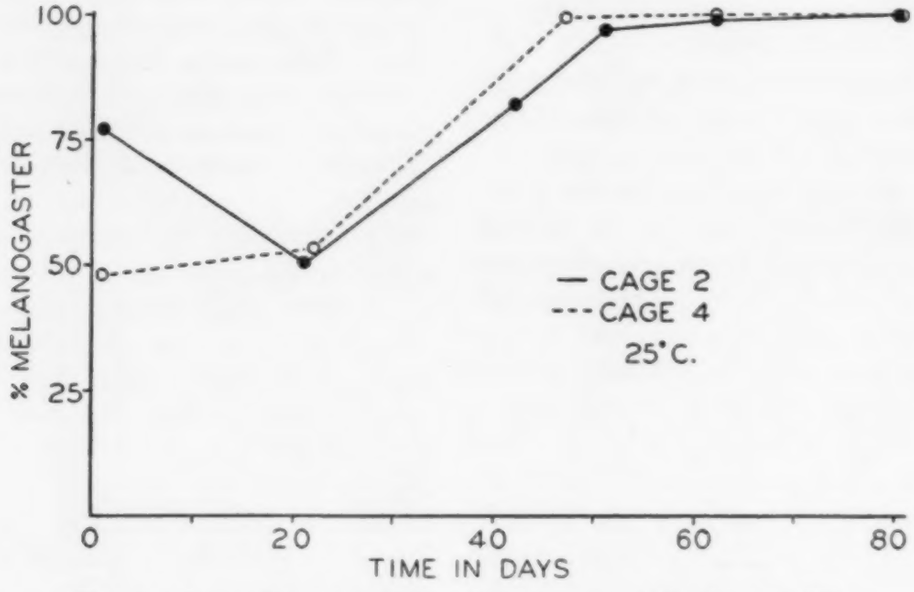

Fig. 1. Competition between *melanogaster* and *simulans* at 25°.

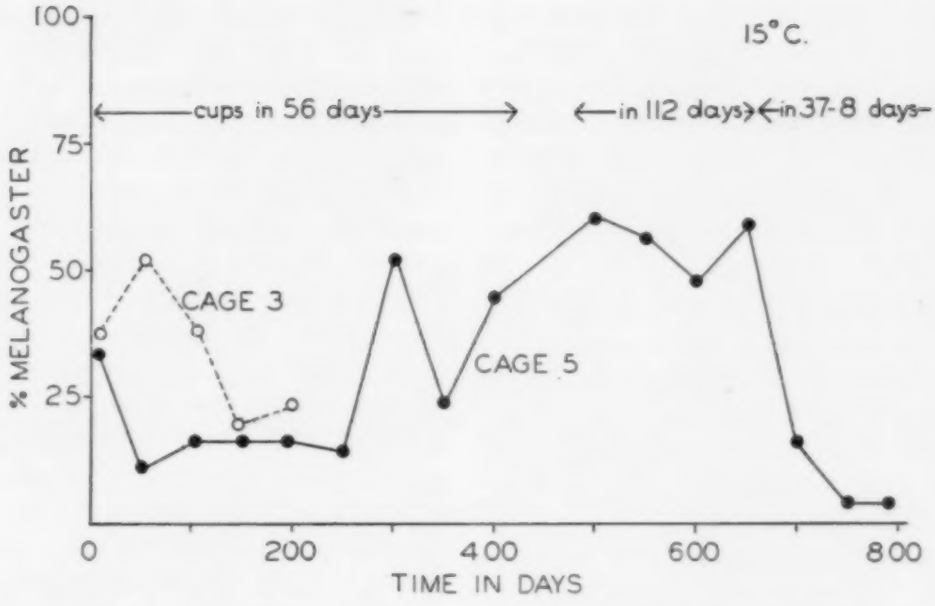

FIG. 2. Competition between *melanogaster* and *simulans* at 15°.

days—24 per cent *mel.* (191). Terminated.

Cage 5: 1 day—33 per cent *mel.* (165); 52 days—11 per cent *mel.* (127); 103 days—16 per cent *mel.* (527); 150 days—16 per cent *mel.* (341); 198 days—16 per cent *mel.* (367); 249 days—14 per cent *mel.* (29); 299 days—52 per cent *mel.* (95); 349 days—25 per cent *mel.* (226); 402 days—45 per cent *mel.* (168).

Clearly there is no elimination of *simulans* and, in fact, it is the more abundant species after more than one year of competition. It is the more successful species at 15° and *melanogaster* is the more successful at 25°. A number of experiments were conducted to shed some light on the nature of this difference.

Although it seemed most unlikely, the difference could be explained on the assumption that *simulans* developed a strain with improved competitive ability in the 15° cages. To test this the adults obtained from the 349 day egg sample of cage 5, which consisted of 25 per cent *melanogaster* and 75 per cent *simulans*, were used to start cage 5B. This was kept at 25° and the cups changed at the rate of 4 per week.

Cage 5B: 18 days—42 per cent *mel.* (366); 25 days—53 per cent *mel.* (434); 50 days—98 per cent *mel.* (264); 82 days—100 per cent *mel.* (64).

From the results of cage 5B it was concluded that the *simulans* in cage 5 had not developed improved competitive ability but that the difference between the 15° and 25° cages was a temperature effect.

A second possibility was that the relative fecundity of *simulans* and *melanogaster* at 15° and 25° might be different. To test this hypothesis a cage was filled with 200 *melanogaster* and 200 *simulans*. Equal numbers of males and females were used. The *melanogaster* were of stock 99 and the *simulans* of stock 75. Both had previously been cultured in bottles. The cage was put at 25° with two food cups. After one day these cups were removed and the entire surface of each was divided and put into 4 standard fly bottles with food. This gave the first 25° sample. The cage was then placed at 15° with two food cups. After a period of one day for adjustment these two cups were removed and two fresh ones added. These were left for one day and then removed and the surface of each divided and put into 4 regular fly bottles with food. This gave

the first 15° egg sample. The cage was then put at 25° for the second sample at this temperature and finally at 15° for the second 15° sample. In every case one day was allowed for the flies to become adjusted to the temperature before the egg sample was taken. The results were as follows:

First 25° sample—53 per cent *mel.* in a total of 534 males.
Second 25° sample—44 per cent *mel.* in a total of 919 males.
First 15° sample—88 per cent *mel.* in a total of 142 males.
Second 15° sample—82 per cent *mel.* in a total of 143 males.

These results show not only the retarding influence of low temperature on oviposition, as seen by the greatly reduced total number of eggs, but indicate that *simulans* lays relatively fewer eggs than *melanogaster* at 15°. Therefore, the superiority of *simulans* in the 15° cages cannot be due to its greater fecundity in fresh cups.

A third possibility was that the rate at which cups were replaced might be affecting the outcome of competition. It had previously been noted that *simulans,* in pure culture, develops slightly faster than *melanogaster* at 25°. If this relation held at 15°, perhaps the schedule of changing cups at the rate of 2 per week (each cup in the cage for 56 days) was such that only a small proportion of the *melanogaster* could emerge. That something of this sort is involved is indicated by the following experiment. Three cups were placed in a 25° cage with a full size population which was giving approximately equal numbers of *melanogaster* and *simulans* eggs. These cups were left in the cage for one day during which they became coated with eggs. The cups were then placed in an empty cage at 15°. Shortly before the first adults were expected, the cups were taken from the cage and placed in wide glass cylinders with a gauze cover. The adults were removed and counted daily (this prevented any later generations from developing in the cups). Under these conditions *simulans* and *melanogaster* have markedly different emergence peaks. *Simulans* males first appeared on the 30th day and 87 per cent emerged between 36 and 47 days after oviposition. *Melanogaster* males first appeared on the 39th day. The bulk of emergence came later, 76 per cent emerging between the 58 and 72 days.

It should be remembered at this point that each cup remained in the 15° cages for 56 days. The data from the three cups show that 91 per cent of the *simulans* males and 14 per cent of the *melanogaster* males emerged prior to 56 days. This is thought to be the main reason why *melanogaster* remained at a low percentage in the 15° cages.

If the 2 per week rate of exchanging cups was responsible for the failure of *melanogaster* to make a better showing, replacing cups at the rate of 1 per week should make conditions more favorable for this species. The original cage 5 population was still available and on the 478 day approximately 900 adults (50 per cent *melanogaster* and 50 per cent *simulans*) were put into a fresh cage. The cups were replaced at the rate of 1 per week, which meant that each cup was in the cage for 112 days.

Cage 5 (cont.): 500 days—60 per cent *mel.* (163); 550 days—56 per cent *mel.* (215); 600 days—48 per cent *mel.* (179); 650 days—59 per cent *mel.* (168).

Under these conditions *melanogaster* possibly fared better but it did not eliminate *simulans* as was expected. The probable reason for this was the abundant growth of molds that formed in the cups when they were kept for so long in the cages. The cups were generally free of heavy mold growth during the first 60 days. It is in this period that most of the *simulans* emerge. Cups older than 60 days were covered nearly always by a heavy mold growth. It should be recalled that most of the *melanogaster* emerge between 58 and 72 days. It is believed that

the mortality of the late emerging flies is definitely increased as a result of mold. If the growth of mold could be prevented, it should be possible for *melanogaster* to eliminate *simulans* at 15° when the cups are changed at the rate of 1 per week.

On the 652 day, cage 5 was subjected to a new experimental procedure. An attempt was made to eliminate *melanogaster* through frequent exchange of cups. The new rate was 3 cups a week (Tuesday 1, Thursday 1, Saturday 1). Each cup was in the cage for 37–38 days. The experiment was so designed that only those adults emerging from cups in less than 37–38 days contributed to the new population. The anticipated drop in the frequency of *melanogaster* occurred but this species was not eliminated by the time it became necessary to discontinue the experiment.

Cage 5 (cont.): 700 days—16 per cent *mel.* (166); 750 days—4 per cent *mel.* (223); 790 days—4 per cent *mel.* (201).

B. Effects of Frequent Cup Changes at 25°

The 15° experiments, just described, suggested that the frequency with which cups are added and removed from cages can be used to influence the results of competition between *melanogaster* and *simulans*. When cups are in the cages for short periods of time the faster developing *simulans* are favored.

In the following experiment an attempt was made to favor *simulans* in its competition with *melanogaster* at 25°. The adults from the *simulans* 75 stock cage and the adults from the *melanogaster* 99 stock cage were placed in an empty cage. Sixteen food cups were placed in this cage and the adults were allowed to oviposit for 1 day. The cups were then removed and the experimental populations started with cages containing 8 of these cups. A total of 6 cages were started in this manner. When the adults began emerging fresh cups were added. In cages 18 and 21 the schedule was 4 per week (Tuesday 1, Thursday 1, Saturday 2). This is the usual rate for cages kept at 25° and each cup remains in the cage for 28 days. In cages 19 and 22 the schedule was 5 per week (Tuesday 2, Thursday 1, Saturday 2). These cups were in the cages for 20–24 days. Cages 20 and 23 had their cups changed at the rate of 6 per week (Tuesday 2, Thursday 2, Saturday 2) for the first 75 days. Thereafter the cups were replaced at the rate of 8 per week (Tuesday 3, Thursday 2, Saturday 3). When the rate was 6 a week each cup was in the cage for 18 to 19 days. When the rate was 8 per week each cup was in the cage for 14 days.

On the 43rd day the adults of all cages were destroyed and the population was reconstituted with the adults emerging after 43 days. This procedure was necessary to eliminate those adults that emerged from the cups that started the populations.

Table 1. *The effect of rate of cup exchange on competition between* melanogaster *and* simulans

		Days after start of experiment									
		25		50		75		100		125	
Cage	Cups exchanged	% *mel.*	Total ♂	% *mel.*	Total ♂	% *mel.*	Total ♂	% *mel.*	Total ♂	% *mel.*	Total ♂
18	4 a week	27	258	67	177	80	182	96	459		
21	4 a week	57	200	83	157	92	200	93	368		
19	5 a week	44	210	92	210	90	180	98	543		
22	5 a week	47	265	97	227	97	189	99	294		
20	6 a week	52	183	76	131	91	213	—	—	—	—
	8 a week							94	475	98	153
23	6 a week	52	228	78	141	85	250	—	—	—	—
	8 a week							91	201	92	257

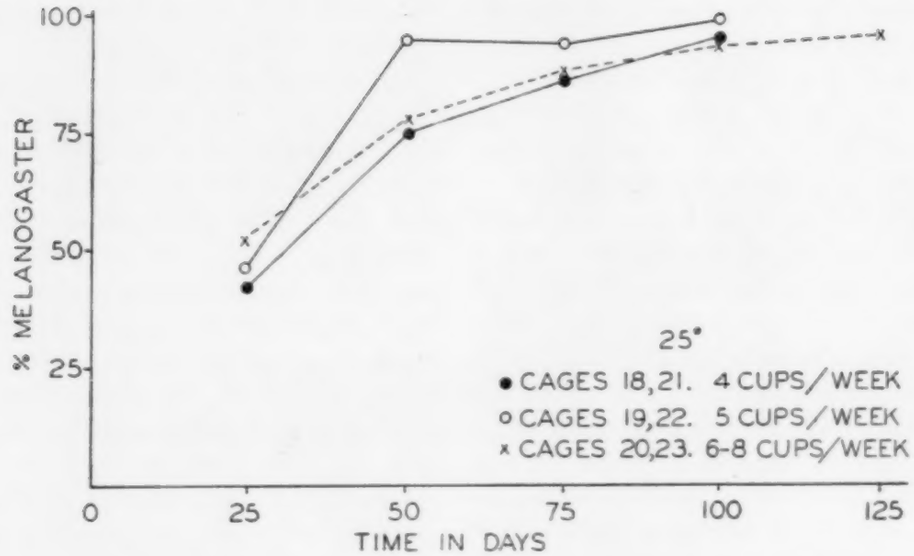

FIG. 3. The effect of rate of cup exchange on competition between *melanogaster* and *simulans* at 25°. Data from table 1.

Many of these would have had a longer time to develop than called for by the scheduled rate of cup replacement. In a similar way the adults of cages 20 and 23 were destroyed on the 76 day, when the schedule was changed from 6 to 8 cups per week.

The results are given in table 1 and figure 3. There is no evidence that *simulans* is favored by an increased frequency of cup exchange. This finding was unexpected in light of the 15° experiments. There is, however, a simple reason for the different results at 15° and 25°. It will be remembered that, in cups containing embryos of both species, *simulans* develops more rapidly than *melanogaster* at 15°. At 25° this proved not to be the case. Both in bottles and in the cups of population cages containing embryos of both species, *simulans* develops slightly slower than *melanogaster*. .One example of this

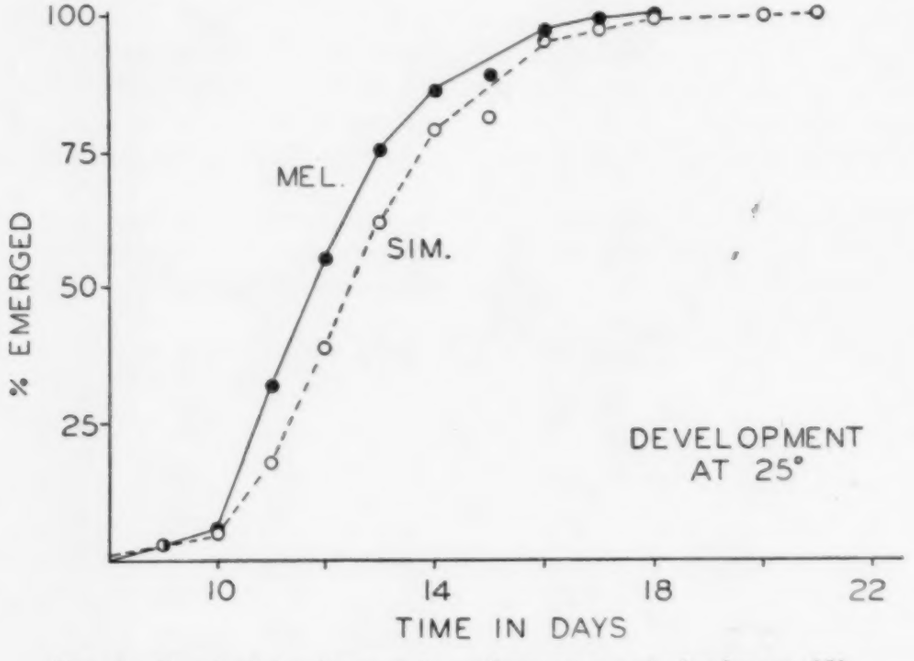

FIG. 4. Speed of development in *melanogaster* and *simulans* at 25°.

will be given. Four cups were put in a cage containing 1,135 adults of which 78 per cent were *simulans* and 22 per cent *melanogaster*. The cups were left for 1 day and then transferred to an empty cage. When the adults began to appear they were removed from the cages daily and classified. The results are shown in figure 4. The fact that *melanogaster* is the faster developing species at 25° indicates that an increased rate of cup exchange might be expected to favor it slightly.

These results seem to give a ready explanation for the different effects of rate of cup exchange at 15° and 25°. At the lower temperature *simulans* develops considerably faster than *melanogaster* and a rapid rate of cup exchange has the expected effect of increasing its frequency. At 25° the tempo of development of *melanogaster* is slightly more rapid and a faster rate of cup exchange naturally does not favor *simulans*.

C. The Length of Time Eggs Are Deposited in Cups

The following experiment was designed to learn if *simulans* and *melanogaster* would oviposit with equal readiness in cups that already contained eggs or larvae. A population cage of *simulans* and one of *melanogaster* served as egg sources. Food cups were placed in one of the cages for 1, 2, or 4 days and then removed and placed in the cage of the other species for approximately the same length of time. The cups were then removed and the surface food, containing eggs or larvae, was put in regular fly bottles with food. The experiment was conducted at 25°. The adult males that emerged were classified. The results are given in table 2.

There is a marked difference in the behavior of the two species. *Melanogaster* will lay in cups where *simulans* eggs and larvae are already present. On the other hand, practically no *simulans* appeared in cups which had previously been in a *melanogaster* cage for 2 or 4 days.

This difference between *melanogaster* and *simulans* would seem to be of considerable importance in the outcome of competition so an additional experiment was performed to check the conclusion. A mixed population consisting of 1,135 adults of which 78 per cent were *simulans* and 22 per cent were *melanogaster* was put in a cage with 4 food cups. After 4 days these were removed and placed in a cage that will be called the "4 day cage." Four fresh cups were then put in with the adults and left for 1 day. These were removed and placed in the "1 day cage." Finally, 4 additional cups were put in for a period of 7 days to give the "7 day cage."

Table 2. *The effect of oviposition by one species on subsequent oviposition by another*

Cup	Schedule	Total ♂	% mel.
A	1 day *sim.* then 1 day *mel.*	106	60
B	1 day *sim.* then 1 day *mel.*	118	54
E	2 days *sim.* then 2 days *mel.*	82	37
F	2 days *sim.* then 2 days *mel.*	89	48
I	4 days *sim.* then 5 days *mel.*	70	26
J	4 days *sim.* then 5 days *mel.*	48	54
C	1 day *mel.* then 1 day *sim.*	100	100
D	1 day *mel.* then 1 day *sim.*	99	87
G	2 days *mel.* then 2 days *sim.*	121	100
H	2 days *mel.* then 2 days *sim.*	110	100
K	4 days *mel.* then 5 days *sim.*	80	99
L	4 days *mel.* then 5 days *sim.*	102	100

When the adults began appearing, they were removed from the cage daily. This was done to minimize the risk of these adults depositing eggs. The cups were checked frequently after the 14th day. No fresh eggs or larvae were noted in the 1 day cage. Several young larvae were seen in the 4 day cage on the 22nd day and in the 8 day cage on the 17th day. It was clear, however, that the possibility of counting the second generation adults was so slight that it could be disregarded.

The results were as follows. The 1 day cage produced 744 females and 814 males of which 28 per cent were *melanogaster*. The 4 day cage produced 1,177 females and 1,107 males of which 29 per cent were *melanogaster*. The 7 day cage produced 1,049 females and 1,019 males of which 41 per cent were *melanogaster*.

The 1 day cage and the 4 day cage seem to give an identical result as far as relative numbers of the two species are concerned. In the 7 day cage, on the other hand, the expected greater frequency of *melanogaster* was observed.

It is proper at this point to refer again to Sturtevant's (1920) belief that *simulans* fares somewhat better than *melanogaster* in old cultures. A complete study of this point has not been made but two experiments would seem to indicate that it is not true for the strains and conditions that I have used. They will now be described.

In most experiments conducted at 25° the cups are in the cages for 28 days. Eggs are deposited in the cups shortly after they are placed in a cage. Several days later a mass of nearly uniform size larvae will be observed. Somewhat later the surface of the cups will seem to consist entirely of pupae. Adults begin emerging from these on the 8th or 9th day and this process will continue for some days. In a cup 14 days old, young larvae may be seen, and, as the cup ages, their number may increase. If Sturtevant's suggestion is correct one might expect these old cups to favor *simulans*. The following experiment was carried out to test it. The old cups that were being removed after 28 days from cage 13 were placed in an empty cage-13A. Cage 13 had a population that was giving 84 per cent *melanogaster* and 16 per cent *simulans* when egg samples were taken in the usual manner. If the old cups favored *simulans*, we would expect its frequency to be greater than 16 percent. The old cups were transferred from cage 13 to 13A at the rate of 4 a week. On the 12th day cage 13A had about 800 adults and an egg sample gave 98 per cent *melanogaster* (287 males counted). On the 23rd day another egg sample gave 100 per cent *melanogaster* (91 males counted). On the 24th day the adults were counted. Of the 340 males present 97 per cent were *melanogaster*. Under the conditions of this experiment it would appear that old cups are more favorable to *melanogaster* than to *simulans*.

Still another test was made as follows. In cage 14 a mixed population was allowed to deposit eggs in 8 cups for 1 day. These cups were then put in an empty-14A cage. Adults began appearing on the 9th day and the cups were available for these adults to oviposit until the 18th day. The adults were then removed, counted, and discarded. It was found that of the 125 males, 86 per cent were *simulans* and 14 per cent were *melanogaster*. On the 19th day two adults were found in the cage. Beginning on the 22nd day the adults were removed approximately every 7 days, counted, and discarded. These same cups continued to give adults until the experiment was terminated on the 64th day. The percentage of *melanogaster* in the total males counted was as follows:

Cage 14A. 22 days—6 per cent *mel.* (217); 29 days—15 per cent *mel.* (149); 36 days—29 per cent *mel.* (277); 44 days—26 per cent *mel.* (190); 50 days—24 per cent *mel.* (323); 57 days—45 per cent *mel.* (111); 64 days—83 per cent *mel.* (60).

Once again it appears that *melanogaster* is favored over *simulans* in old cups.

These experiments are not necessarily a refutation of Sturtevant, since it should be remembered that he was speaking of competition in bottles and the present experiments were conducted in cages. In addition, the strains were of different origins.

D. Oviposition Sites of the Two Species

In the early experiments egg samples were secured by placing a food cup in a cage for 1 day (at 25°). At the end of this time the cup was removed. If the population was of maximal size when the sample was taken, the entire surface of the cup would be white from hundreds of eggs deposited. Four small areas of the surface food would be cut out and each placed in a standard half pint fly bottle with food. It was often noted that the relative num-

bers of the two species differed widely among the four subcultures. This suggested that the surface of a food cup might not be a single niche as far as egg laying of the two species is concerned. Records were kept, therefore, of the exact position in the cup from which the subsamples were taken.

It was seen that both species find the edge of the cups the most desirable place to lay eggs. Thus, when the cup has been in the cage for a few hours there will be many eggs at the edge and only a few in the middle. In addition, it was found that *simulans* will deposit eggs in the center more readily than *melanogaster*.

Another factor influencing oviposition is the type of food surface. When the food cups are prepared, the hot food is poured in while in a semi-liquid condition. Upon cooling this solidifies and a crust is formed. Before these cups are placed in a population cage, the surface crust is normally removed. If the two species are given a choice between the cups with crust ("old surface") and without crust ("fresh surface"), they greatly prefer the latter. It was found, however, that *simulans* will deposit its eggs on the old surface cups more readily than will *melanogaster*.

Both of the above points are brought out in the following experiment which was conducted at 25°. Four cups were put into each of two cages that were giving approximately 60 per cent *simulans* and 40 per cent *melanogaster*. Two of the cups in each cage were old surface cups and two were fresh surface cups. After 1 day the eight cups were removed. Four subsamples were taken from each of the eight cups. Two were from the edge of the cup and two from the center. The subsamples were placed in standard fly bottles with food. The results are given in table 3.

TABLE 3. *The effects of surface type and position in the cup on oviposition*

	Old surface	Fresh surface	Totals
Center of cup	*Sim.* 255 (74%) *Mel.* 90 (26%)	*Sim.* 225 (63%) *Mel.* 131 (37%)	*Sim.* 480 (68%) *Mel.* 221 (32%)
Edge of cup	*Sim.* 230 (61%) *Mel.* 150 (39%)	*Sim.* 122 (41%) *Mel.* 179 (59%)	*Sim.* 352 (52%) *Mel.* 329 (48%)
Totals	*Sim.* 485 (67%) *Mel.* 240 (33%)	*Sim.* 347 (53%) *Mel.* 310 (47%)	

In the situation preferred by both species, namely, the edge of fresh surface cups, the frequency of *melanogaster* is 59 per cent. The data show that *simulans* is not deterred by the centers of cups, or the old surfaces, so much as is *melanogaster*. In the situation least favorable to *melanogaster*, namely the centers of old surface cups, its frequency drops from 59 per cent to 26 per cent.

TABLE 4. *The effect of selection for type of food surface and oviposition site on competition between* melanogaster *and* simulans

	Old surface—center				Fresh surface—edge			
	Cage 14		Cage 16		Cage 15		Cage 17	
Selection	Per cent *Mel.*	Total ♂	Per cent *Mel.*	Total ♂	Per cent *Mel.*	Total ♂	Per cent *Mel.*	Total ♂
1st	51	297	30	488	65	711	61	566
2nd	43	361	13	265	73	596	70	798
3rd	33	571	13	452	74	239	81	761
4th	54	173	6	359	86	355	93	644
5th	44	953	5	333	85	1087	94	965
6th	39	521	7	501	86	516	94	358
7th	40	911	2	729	93	541	99	732
8th	34	854	0	642	97	979	99	773
9th	22	581	—		98	927	99.8	862
10th	13	487			99	799	99.8	592
11th	14	125			99	426	100	223
12th	3	556			100	604		
13th	4	467			—			

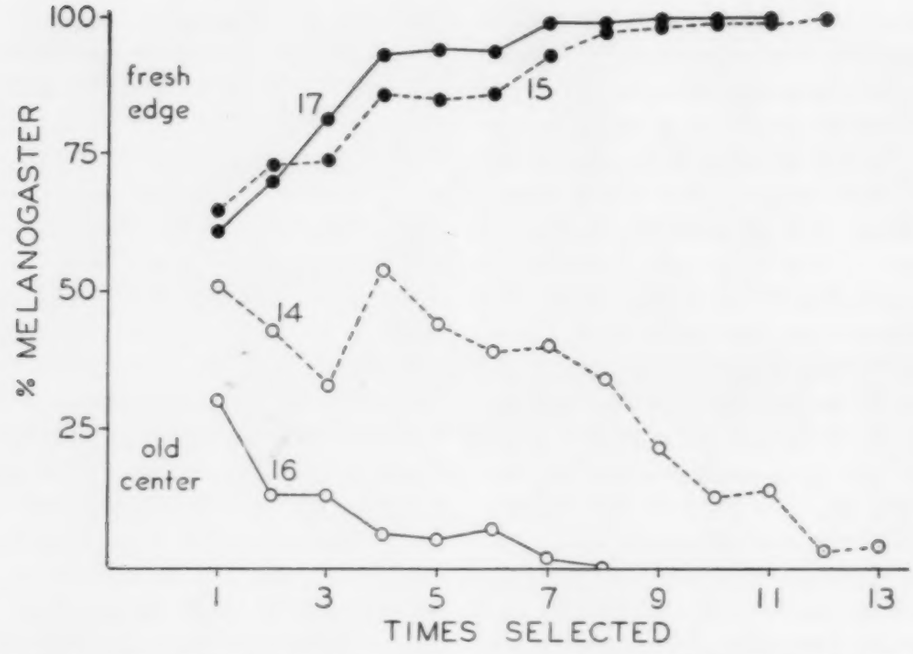

FIG. 5. The effect of selection for type of food surface and oviposition site on competition between *melanogaster* and *simulans*. Data from table 4.

E. MODIFICATION OF THE COURSE OF COMPETITION THROUGH SELECTION OF FOOD CONDITIONS

The data just given on the differential utilization of food conditions by *simulans* and *melanogaster* suggested a means of modifying the outcome of competition between the two species. The following experiment, which was conducted at 25°, indicated that this could be done.

Approximately equal numbers of *simulans* from stock cage 75 and *melanogaster* from stock cage 99 were put into one population cage. The total number of adults was well over a thousand. Eight old surface cups and 8 fresh surface cups were put into the cage. At the end of one day the cups were removed. The food at the edge of the 8 old surface cups was removed and discarded. The center area, with the eggs deposited there, was left intact and these 8 cups were used to begin cage 14. The centers of the 8 fresh surface cups were removed and these cups, having only the eggs laid at the edge, were used to start cage 15. The procedure was repeated, using the same adults, to start cage 16 (centers, old surface) and cage 17 (edge, fresh surface).

On the 9th day adults began appearing in the cages. Food cups were then placed in the cages to provide for the adults. These were changed every 2–3 days so no eggs deposited in them contributed to the adult population. By the 18th day emergence was over and all cups were removed from the cages and discarded. Eight old surface and 8 fresh surface cups were put in. These were left for one day and then removed. In the case of cages 14 and 16, the 8 fresh surface cups were discarded and the edges of the 8 old surface cups were cut out and also discarded. The 8 old surface cups with the centers remaining were then put in an empty cage. The same procedure was followed for cages 15 and 17 except that only the edges of the 8 fresh surface cups were retained. The adults were etherized, classified, and discarded.

Thus, in two cages (14 and 16) there was repeated selection for adults that lay eggs in the centers of the old surface cups. In cages 15 and 17 there was selection for adults that lay eggs at the edge of fresh surface cups. The two fresh surface edge cages contained the environment that both species preferred. On the basis of the

data previously given, we might expect *melanogaster* to eliminate *simulans* because of its innate competitive superiority. (It should be remembered, however, that competition is less severe in this case than in the usual cage experiments. The number of embryos developing in a single cup is much fewer since the cups are available for egg laying during a single day only and many of the eggs are removed when the appropriate portion of the surface food is removed. The end result is a low number of eggs per cup and it is likely that competition for food and space is much reduced.) The two old surface, center cages selected for an environment that neither species preferred but one that *simulans* utilizes more readily than does *melanogaster*. We would expect, therefore, that *simulans* would fare better than it does in the fresh surface, edge cages.

In this experiment population changes were measured by counts of adult males. The results are given in table 4 and in figure 5. They dramatically indicate the tremendous effect resulting from the selection for seemingly slight ecological differences. Without doing an experiment of this sort one would not have imagined that the difference between the food at the edge and the center of a cup, or the difference between food with a thin crust and no crust would be of such importance. The results reveal the inadequacy of such reasoning. In the center of an old surface cup, *simulans* is the "superior" species; at the edge of a fresh surface cup, *melanogaster* is "superior."

Summary and Conclusions

The experiments reported in this paper are the first in a comprehensive program devoted to studying competition between *Drosophila simulans* and *Drosophila melanogaster*. It does not seem necessary at this time, therefore, to make a detailed comparison of the results here reported with those of previous investigators. It might be mentioned, however, that Merrell (1951) and others have described competition between *Drosophila funebris* and *Drosophila melanogaster* and Zimmering (1948) has described competition between *Drosophila pseudoobscura* and *Drosophila melanogaster*.

The peculiar interest attached to competition between *melanogaster* and *simulans* stems from their close morphological, genetic, and ecological similarity. Their co-existance under natural conditions is understandable (at the present) only on the assumption that they do not occupy identical ecological niches.

The experiments reported in this paper have revealed several laboratory conditions that affect the outcome of competition between the two species. In population cages kept at 15°, in which the food cups are replaced at the rate of 2 or 3 a week, *simulans* is the more successful species. In population cages kept at 25°, in which the food cups are replaced at the rate of 4, 5, 6, or 8 times a week, *melanogaster* eliminates *simulans*. Other ecological niches were found in the food cups. *Simulans* is better able to oviposit in the "unfavorable" center of cups and on food having a surface crust. It is even possible to reverse the outcome of competition by taking advantage of these preferences for oviposition sites.

During the course of these experiments it has become apparent that there are many slight differences in the biology of the two species. It is probable that the seemingly "uniform environment" of a population cage may contain many environmental variables that influence competition between *melanogaster* and *simulans*.

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PHYSIOLOGICAL PROPERTIES OF GENE ARRANGEMENT CARRIERS IN *DROSOPHILA PERSIMILIS*. II. WING-BEAT FREQUENCY AND WING DIMENSIONS[1]

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INTRODUCTION

Variation in the third chromosome of *Drosophila* persimilis along an altitudinal transect in the Yosemite region of California consists of a gradient in relative frequencies of the four major gene arrangements (Dobzhansky, 1948; Spiess, 1950). Within each local population these gene arrangements often display different adaptive values indicating that each consists of different alleles in combinations which are most useful to the species in that area. In order to be able to attribute the gradient to genetic or ecological causes or both, it is necessary to analyze the many properties of the gene arrangements and compare the findings from each locality along the transect.

Among the several types of variation which might be controlled by genes on the third chromosome and which might have adaptive significance for insects living along an altitudinal gradient, those pertaining to flight are likely to be of first rank importance. Wing-beat frequency is known to be dependent on many physical and physiological factors such as air temperature, air density, age of insect, sex, species, size of wing, and volume of thoracic musculature (Chadwick and Williams, 1949; Reed, Williams, and Chadwick, 1942; Williams and Reed, 1944). The adaptive significance of variations in wing size and wing-beat frequency is a matter of speculation, however. Certainly compensation for density of air with altitude must be important to the fly from the standpoint of lift efficiency of the wing, a factor conceivably important in general activity, rates of dispersal, sexual activity, energy utilization, and so on. The nature of variation in flight mechanisms over this altitudinal transect is, then, complicated by many considerations, but is nevertheless a source of information which might prove useful in the search for a genetic basis for the gradient in frequencies of gene arrangements.

Flies from three localities carrying the Whitney and Klamath gene arrangements were tested in order to answer the following questions: 1) Do the two arrangements differ in genic content affecting wing-beat or wing size? 2) Does the heterozygous condition for the arrangements confer heterosis to any measurable extent? 3) Is there any change in flight characteristics accompanying increase in altitude?

The strains of *D. persimilis* used for these tests were collected a) during the summer of 1950 by Th. Dobzhansky at Mather (el. 4600′) and Mono Lake (el. 6600′) and b) during February, 1948, by Carl Epling at Jacksonville (el. 850′). Mather and Jacksonville are on the western slope of the Sierra Nevada while Mono Lake is on the eastern slope. (For a description of the areas, see Dobzhansky, 1948.)

MATERIALS AND METHODS

The stroboscope technique devised by Williams and Chadwick (1943) was used to measure the wing-beat frequency. The stroboscope consists of a flash-frequency neon or low-pressure bulb controlled by an electric oscillator. When tuned to synchrony with a cyclic motion, it causes the motion to appear stationary. Thus the moving wings of an insect placed in the path of the light can be made to "stop" and the beat frequency can be read directly

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from a calibrated scale. Individual flies mounted by the abdomen to paraffined strips of paper were inserted into holders so that the animal rested lightly on a small metal platform. The sudden removal of the platform by an electromagnet stimulated the flight reflex; if this reflex was weak, a puff of air usually induced the insect to fly.

All flight measurements were taken in a temperature controlled bath at 20° ±0.5° C., the flies being confined to a glass cylinder immersed in the bath. Flights were of only a few seconds duration, and the frequency noted was the peak attained during that time. Approximately ten to fifteen readings were made on each fly with a twenty second interval between flights to avoid the effects of fatigue (Chadwick, 1939).

Flies to be flown were raised as the progeny of single pair matings in half-pint jars kept at 15° C. Since a fly can become habituated to a change in temperature of 10° in less than thirty seconds (Chadwick, 1939), this brief change from the culture conditions to flight conditions should have had no effect on the wing-beat. Only virgin females five to seven days old were used. Flies were made homozygous for the gene arrangement in question by crossing strains known to be homozygous, and heterozygotes were derived by using F_1 adults as parents.

Wing measurements of the several zygotic combinations were made using flies from the flight experiments in order to determine any morphological variation paralleling the changes in wing-beat frequency. The method used was similar to that developed by Reed and Reed (1948). Wings were removed and mounted temporarily in glycerin and projected on squared paper from which the wing dimensions could be accurately taken. The dimensions found to be most useful were the following: area, length, (from tip of longitudinal vein III to junction of anterior crossvein and 1. v. IV), length 2 (overall from tip to wing articulation) and width (perpendicular to length through junction of posterior crossvein and 1. v. V). An index having a definite relation to the mechanics of flight has been derived by Reed, Williams, and Chadwick (1942) and is used here both because it magnifies small differences and because areas or lengths alone may overlap. It is calculated by multiplying the wing area (mm^2) by the cubed length (mm^3). This value when multiplied by the wing-beat frequency squared gives a value proportional to the stroke-energy, or kinetic energy, of the air volume put in motion by the moving wings.

In all cases at least three strain crosses were made for each zygotic combination and at least four females from each cross were tested and measured. Fisher's analysis of variance was employed to test for homogeneity of data between strain crosses of the same zygotic combination. In all cases the amount of variability between those strain crosses was not significantly greater than that resulting from random factors.

Experimental Results

Wing-beat frequency:

The strains from Jacksonville were used for two experiments; the first to determine any difference between the wing-beat of the carriers of WT/WT, KL/KL, and WT/KL consists of data from F_1 individuals of strain crosses; and the second to test for increased vigor by using a "double hybrid cross" (mating the F_1 adults obtained by any two first crosses) as would be expected were the original strains maintained by inbreeding methods. Heterozygotes for the gene arrangements in each case were obtained by crossing the progeny of the preceding homozygote cross.

The first homozygote crosses from Jacksonville show a significant difference in wing-beat between the WT and KL arrangements of the order of 500 cycles per minute (see table I, compare No. 1 and No. 3), WT being the faster flier. Gene arrangement heterozygotes fly about as fast as WT; certainly there is apparent

TABLE I. *Wing-beat frequency in double beats per minute*

The "stroke energy" index is obtained by multiplying Reed's index by the wing-beat frequency squared. Standard errors for mean wing-beat frequencies are given. Each mean value is the average of at least three means representing three strain crosses for each genotype.

Type of parent	No. flown	Wing-beat	Stroke energy index
Jacksonville			
(1) $WT_1 \times WT_2$	12	10823±51	1114
(2) $WT_1/WT_2 \times WT_3/WT_4$	12	10826±59	1021
(3) $KL_1 \times KL_2$	20	10349±73	1123
(4) $KL_1/KL_2 \times KL_3/KL_4$	12	10283±58	1015
(5) $WT_1/WT_2 \times KL_1/KL_2$	12	10782±76	1084
(6) Double cross: $WT_{1\times2}/WT_{3\times4} \times KL_{1\times2}/KL_{3\times4}$	24	10624±53	1049
Mather			
(7) $WT_1 \times WT_2$	12	10923±37	1088
(8) $KL_1 \times KL_2$	12	10261±77	1050
(9) $WT_1/WT_2 \times KL_1/KL_2$	16	10727±13	1059
Mono Lake			
(10) $WT_1 \times WT_2$	20	10284±74	936
(11) $KL_1 \times KL_2$	12	10817±74	1035
(12) $WT_1/WT_2 \times KL_1/KL_2$	12	10636±152	1028

dominance for the faster wing-beat over the slower.

In no case did the double hybrid progeny show significantly greater wing beat frequency than the original strain cross F_1. (Compare No. 1 and No. 2, No. 3 and No. 4, No. 5 and No. 6 in table I.) As a matter of fact there is a slight drop in wing beat in two cases when strain cross progeny were mated. Because there was no increase in wing-beat brought about by making such double hybrid crosses, only F_1 individuals were used in subsequent tests.

When the wing-beats of the F_1 from Mather are compared with those from Jacksonville, it is evident that no statistical difference is apparent between them. (Compare No. 1 and No. 7, No. 3 and No. 8, No. 5 and No. 9.) WT/WT averages 500–600 cycles faster than KL/KL in both localities with WT/KL slightly lower than WT/WT.

Strains from Mono Lake, however, do not follow this pattern: There the WT/WT is the lower and almost equal to the wing-beat of KL/KL from localities on the other side of the mountain. The heterozygous combination is intermediate but closer to the higher frequency of the two parental types.

Wing dimensions:

Among the many morphological relationships which are known to influence wing-beat frequency is wing size, a character determined by multiple genetic factors. It is known that wing-beat frequency varies inversely with wing size provided thoracic muscle volume is held constant (Reed, Williams, and Chadwick, 1942).

As in the case of the wing-beat frequencies, the wing dimensions (table II) show WT/WT and KL/KL to be significantly different for Jacksonville and Mather if the F_1 individuals of strain crosses are compared. In these two localities KL/KL has the larger wing than WT/WT with WT/KL slightly smaller than WT/WT in area and width but equal or longer in length. In all cases at Jacksonville the double hybrid cross produced smaller wing size than the first strain cross. (Compare Reed's index for No. 1 and No. 2, etc.)

TABLE II. *Wing dimensions in mm.*

Standard errors for wing area means are given. For all other dimensions standard errors are equal to or less than 0.01 mm.

Type of parent	Wing area (mm^2)	$Length_1$	$Length_2$	Width	Reed's index
Jacksonville					
(1) $WT_1 \times WT_2$	3.13±0.06	2.00	3.12	1.33	95.06
(2) $WT_1/WT_2 \times WT_3/WT_4$	3.07±0.05	1.99	3.05	1.31	87.10
(3) $KL_1 \times KL_2$	3.23±0.03	2.06	3.19	1.39	104.85
(4) $KL_1/KL_2 \times KL_3/KL_4$	3.19±0.04	2.07	3.11	1.35	95.96
(5) $WT_1/WT_2 \times KL_1/KL_2$	3.04±0.02	2.01	3.13	1.31	93.22
(6) Double cross: $WT_{1\times2}/WT_{3\times4} \times KL_{1\times2}/KL_{3\times4}$	3.12±0.03	2.00	3.10	1.34	92.95
Mather					
(7) $WT_1 \times WT_2$	3.09±0.03	2.04	3.09	1.32	91.17
(8) $KL_1 \times KL_2$	3.22±0.03	2.07	3.14	1.33	99.69
(9) $WT_1/WT_2 \times KL_1/KL_2$	3.15±0.04	2.02	3.08	1.33	92.04
Mono Lake					
(10) $WT_1 \times WT_2$	3.09±0.02	2.01	3.06	1.32	88.54
(11) $KL_1 \times KL_2$	3.03±0.03	2.08	3.08	1.30	88.53
(12) $WT_1/WT_2 \times KL_1/KL_2$	3.14±0.03	2.02	3.07	1.33	90.85

The flies from Mono Lake are of a noticeably different pattern: KL/KL is slightly but not significantly smaller than WT/WT with WT/KL still larger but still not as large as KL/KL from the two western slope localities. Reed's index for these from Mono Lake are all about equal.

Attention is called to the fact that the wing dimensions are all slightly larger than those reported by Reed, Williams, and Chadwick for strains of *D. pseudoobscura* Race B, now *D. persimilis*: the average difference in wing area is from 0.3–0.5 mm^2. This discrepancy can be accounted for as follows: 1) the strains used herein come from localities quite distant from those studies by the above authors (the closest locality, Stony Creek, is about 170 miles northwest of the Yosemite area), and it was shown that some local populations differed significantly in wing areas as well as wing-beat. 2) It is known that wing size varies inversely with the temperature during development (Stanley, 1935). The authors above used 20° C. while the present author used 15° C. for raising flies to be flown; the order of magnitude in the difference can be completely accountable by the fact.

"Stroke-energy index":

The right hand column of table I consists of an array of figures which are proportional to the kinetic energy given the air by the stroke of the wings. It is also proportional to the thoracic muscle volume. It represents the relative amount of vigor the fly possesses in respect to its ability to stroke through the atmospheric conditions encountered.

It will be seen that for the flies at Jacksonville the F_1 individuals of WT/WT and KL/KL strain crosses respectively have indices nearly equal (KL is about 1% higher than WT), while the WT/KL first cross individuals are about 3% lower. It is interesting to note that the double hybrids all show 10% lower indices in the case of WT/WT and KL/KL while WT/KL is about 4% lower than the first WT/KL.

At Mather WT/WT seems about equal to WT/KL from Jacksonville, that is lower than WT/WT from Jacksonville,

with KL/KL equal to WT/KL both about 3% lower than WT/WT. In other words the amount of stroke energy for these F_1 individuals from Mather is consistently lower than the same corresponding arrangement combinations from Jacksonville.

At Mono Lake WT/WT is 10% lower than KL/KL with WT/KL about equal to KL/KL, but all combinations are lower than those corresponding in the two preceding localities.

Discussion

In a search for genetic factors which might have adaptive value for a winged insect occupying an altitudinal transect, *a priori* reasoning would lead us to suspect adaptive differences in the flight mechanism between populations inhabiting different altitudes. It is known that wing-beat frequency varies inversely with air density (Chadwick and Williams, 1949). The normal limits of air pressure over the altitudinal transect in question (and consequently the air density), from sea level to ten thousand feet drop about 30%. Under experimental conditions a drop in air density corresponding to that of the transect increases the wing-beat frequency about 500 cycles (*D. repleta*). Chadwick and Williams found, however, that wing-beat frequency varied less through the range of air densities than might be expected if both power output and stroke volume were to remain constant. They found that stroke amplitude decreased at higher densities while angle of attack was altered at low densities to compensate for differences in the air. In other words insect flight appears to be a homeostatic mechanism in that wing motion can be altered by many anatomical and physiological factors all of which interact to compensate for density changes.

If we examine the data from Jacksonville alone it is evident that while WT/WT and KL/KL flies have different wing-beat frequencies, their wing sizes are also different and compensate in such a way that the power output for the two zygotic combinations is about the same for each. At Mather the homozygote combinations differ in the same way and their power output is nearly equal, although all are consistently lower than their corresponding genotypes from Jacksonville. At Mono Lake WT/WT are definitely poorer fliers than KL/KL under these experimental conditions since there is about a 10% difference between them. If the same genotypes from the three localities are compared, therefore, we can see an apparent loss in power output with increase in altitude; but the differences are so slight that they might be suspect as nonsignificant if it were not for their consistency.

To summarize this phase of the problem, the homozygous forms differ in wing-beat frequency and inversely in wing size from both localities on the western slope; however, the same homozygous types from the eastern slope locality have wing-beat frequencies reversed with respect to those from the western slope with wing sizes equal, and thereby can be considered racially distinct for such characteristics. Heterozygotes are in all respects intermediate or at most slightly below the homozygotes displaying greater expenditure of energy. Whether this intermediacy of the heterozygotes is of the most efficient and therefore heterotic, or adaptively superior, value for the fly in nature has not been tested; but since the heterozygote stroke energy indices are all but slightly different from the homozygote indices, it seems unlikely that any marked heterotic effect is displayed here.

There is an aspect of these results which may possibly have a bearing on the problem of heterosis exhibited here: flies from Jacksonville were not only F_1 adults from strain crosses but also the progeny of crosses between different F_1's, the latter being doubly hybrid. Although the wing-beat frequency of both WT and of both KL crosses are equal, wing size drops significantly in both cases with a concomitant drop in stroke energy index. If the original strains had been maintained by in-

breeding the opposite result would be expected; that is, double hybrids should manifest more vigor than the first hybrids. The fact that no luxuriance resulted from the double hybrid mating indicates two things therefore: homozygosis has not become extensive within strains as would be the case after inbreeding (the strains are maintained by mass matings in which genetic heterogeneity is encouraged), and second the genetic composition of the various F_1 progenies must be more similar, or uniform, than one would otherwise expect since the phenomenon of decreased vigor is apparently such as that accompanying the inbreeding of a heterotic F_1.

In the case of egg-laying capacity and longevity for these strains, heterozygotes were obtained by the method of mating strain cross F_1 adults, and clear evidence of increased vigor was displayed (Spiess, Ketchel, and Kinne, 1952). In the present paper heterozygote arrangements were obtained in the same manner but no increased vigor resulted. However, if the same type of mating is compared in table I (No. 2, No. 4, and No. 5), it is evident that the heterozygous arrangement has a slightly higher stroke energy than those homozygotes obtained by mating strain cross F_1's. Even so the value of stroke energy index is only slightly higher for the heterozygotes than for the double hybrid homozygous arrangements. Certainly then any vigor effect due to heterozygosity of alleles in the inversion heterozygote must be very weak indeed. The higher stroke energy found for the strain cross F_1's must then be due to luxuriance in the remainder of the genome or at least to heterozygosity of alleles other than those affected by the third chromosome gene arrangements.

Summary

(1) *Drosophila persimilis* homozygous for the Whitney or Klamath gene arrangements of the third chromosome although heterozygous genetically differ in wing-beat frequency and in wing dimensions. WT flies from 850 ft. and from 4,600 ft. elevation on the western slope of the Sierra Nevada of the Yosemite region average 10,800–10,900 cycles per minute while KL flies from those localities average 10,250–10,350 cycles per minute. Heterozygotes from the two arrangements average 10,700–10,800 cycles per minute.

(2) WT flies from 6,600 ft. elevation on the eastern slope of the mountains average 10,300 cycles per minute while KL average 10,800; heterozygotes are about 10,650.

(3) WT from the western slope localities have a smaller wing size than KL from those areas: WT averages 3.09–3.13 mm^2, KL about 3.22 mm^2, with heterozygotes resembling WT at 3.04–3.15 mm^2.

(4) WT and KL are not significantly different in wing size at the 6,600 ft. elevation. The heterozygote has the largest wing size of the three zygotic types. KL averages 3.03 mm^2, WT 3.09 mm^2, and WT/KL 3.14 mm^2.

(5) Owing to the differences between these measurements for populations from western and eastern slope localities, it is noted that they are racially distinct, the same gene arrangement from the two slopes giving different wing dimensions or beat frequency.

(6) An index derived from other authors expresses a value proportional to the energy given the air by the wing motion. This "vigor" index decreases consistently with increasing altitude but only slightly. There is no evidence that wing-beat itself changes with increase in altitude in any significant way.

(7) There is no clear evidence that heterozygosis of these arrangements confers heterosis for the characters measured.

(8) The first generation after strain crossing has a higher stroke energy index than the generation resulting from mating the F_1 adults which would indicate that the original strains are not extensively homozygous and also that the genetic composition of the various F_1 progenies must be quite similar since vigor decreases immediately just as if a single heterotic F_1 were being inbred.

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GENETICS OF MARGINAL POPULATIONS OF *DROSOPHILA WILLISTONI* [1]

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Introduction

Since Darwin, one of the most fundamental tenets of theories of evolution has been that hereditary variation present in natural populations furnishes the raw materials from which evolutionary changes may be compounded by selection and other agencies. Representatives of most species of Drosophila are phenotypically fairly uniform in their natural habitats. Nevertheless, genetic analysis of natural populations of Drosophila has shown that they carry great stores of genetic variants. These variants belong mainly to two classes. First, there are variations in the gene arrangements, due chiefly to inversion of blocks of genes. Secondly, all populations studied in this respect carry more or less extensive supplies of recessive mutant genes which, when homozygous, affect physiological and often also morphological properties of their carriers (reviews in Spencer, 1947, and Dobzhansky, 1951).

The magnitude of the store of genetic variants carried in a population should theoretically depend on the breeding structure of that population and on the environment which it inhabits. Thus, the equilibrium frequencies of recessive deleterious mutants should, other things being equal, be lower in small inbred populations than in large panmictic ones (Wright, Dobzhansky, and Hovanitz, 1942). The extent of the chromosomal polymorphism may, on the other hand, be a function of the variety of adaptive niches which a species has mastered in different parts of its geographic distribution area (da Cunha, Burla, and Dobzhansky, 1950).

The study of the interrelationships between the genetic variation in natural populations and the environment in which these populations live has only begun. Many problems in this field await investigation. One such problem is comparison of the genetic variability of populations which live near the center and at the periphery of the distribution area of the same species. The present article reports the results of a genetic analysis of samples from two peripheral populations of *Drosophila willistoni*. These peripheral populations are then compared with populations which live near the center of the species distribution, as well as with other marginal populations.

D. willistoni is a very common species in the American tropics. Its distribution area extends from somewhat south of Buenos Aires, Argentina, where it has recently been collected by Professor C. Pavan (personal communication), to the West Indies and Florida (Patterson, 1943; Burla *et al.*, 1949). According to a private communication from Doctor Harrison D. Stalker, the distribution area reaches northward at least as far as St. Petersburg, Florida. Da Cunha *et al.* found that the populations of *D. willistoni* in central Brazil are large, occur in diverse habitats, and carry the greatest store of genetic variants, particularly inversions. Central Brazil is supposed by these authors to represent the species' center of origin or, at any rate, the region of its greatest differentiation. A comparison of Florida and Cuban populations with those

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of central and southern Brazil will therefore be of interest.

Material

A sample of a natural population of *D. willistoni* was collected on fermenting banana and on naturally occurring fruits at Lake Placid, Florida. Another, but very small, collection was obtained in a similar manner at Soledad Central, Cienfuegos, Cuba. The sexes were separated in the field and brought to New York for analysis.

Variation in the Gene Arrangement

Single wild females were allowed to oviposit in one-half pint culture bottles containing banana agar. Temporary mounts were made of the salivary glands of one or more mature larvae from each culture. The glands were stained in acetic orcein. After a favorable cell was selected by a cursory examination under low magnification, the gene arrangements were determined under a 1.30 N.A. oil immersion objective, using 10× oculars. Since most inversions in *D. willistoni* are short and the species is not very favorable for salivary gland chromosome analysis, it was practical to determine only inversion heterozygotes. For statistical purposes the gene arrangements in the chromosomes of only a single larva from each culture were recorded.

The data on the kinds of gene arrangements found in the populations studied are summarized in table 1. From the Cuban material only 10 flies were tested; in six cases the larvae selected for examination were females. The Florida collection yielded 104 tested flies; in 70 cases the larvae selected were females. Thus, the gene arrangements were determined in a larger number of autosomes than of X-chromosomes.

In all, eleven different inversions were found in the Florida material, and six in the much smaller Cuban sample. The total number of kinds of inversions found in Florida and Cuba is thirteen. With a single exception, all of the gene arrangements discovered in Florida and Cuba were previously described from various localities in central and southern Brazil by da Cunha, Burla, and Dobzhansky (1950). Twelve of the inversions, which are recorded in the Florida and Cuban populations, have been shown by these investigators to be widely distributed in most of Brazil. Considering the species as a whole, nearly all of these twelve inversions are among the most common gene arrangements in their respective chromosomes. Inversion *IIR–D*, however, has been detected only at Mogi, state of São Paulo, and in Florida. The only inversion which so far seems to be endemic in Florida is inversion *A–1* in the third chromosome. This is the most proximal inversion yet discovered in the third chromosome. It extends from the middle of section 87 to include section 92. (For a map showing the numbered regions of the salivary gland chromosomes of *D. willis-*

Table 1. *Frequencies (per cent) of inversion heterozygotes in the Florida and Cuban populations studied*

Inversions	Florida	Cuba
X–L Chromosome		
None	100.0	66.7
D	—	33.3
X–R Chromosome		
None	98.6	100.0
A	1.4	—
Females studied	70	6
II–L Chromosome		
None	46.2	60.0
A	29.8	20.0
E	35.6	30.0
F	—	10.0
II–R Chromosome		
None	53.8	50.0
A	12.5	—
C	1.0	—
D	1.0	—
E	38.5	50.0
III Chromosome		
None	38.5	60.0
A–1	1.9	—
A	43.3	—
H	1.9	—
J	34.9	40.0
Flies studied	104	10

toni, see Dobzhansky, 1950.) Inversion *A–1* includes inversions *A*, *B*, and *C*, and either broadly overlaps or includes inversions *D* and *E*. This inversion brings to 41 the total number of kinds of inversions known in this species.

Inversions in the X-chromosomes of the Florida population appear to be very rare. None of the nine inversions found in the left arms of Brazilian X-chromosomes were detected in the Florida flies. The right arm of the X-chromosome of the progeny of only a single Florida female was discovered to be heterozygous for the

FIG. 1. Mean numbers of heterozygous inversions per individual symbolized by diameters of black circles. (Based in part on da Cunha, Burla, and Dobzhansky, 1950; da Cunha, unpublished; and Dobzhansky, unpublished.)

D inversion, which is one of five known in this arm. On the other hand, the *A* inversion occurred in the right arms of the X-chromosomes in two of the six Cuban females examined; none of these females possessed inversions in the left arms of their X-chromosomes. However, the presence of two inversions in the X-chromosomes of so few flies may indicate that the variability of gene arrangements in these chromosomes is greater in the Cuban population than in the Florida population.

The Florida autosomes are much more variable in gene arrangements than are the Florida X-chromosomes. Nevertheless, the kinds of inversions found in the left arms of the second chromosomes of this population are only two of the eight known. In the Florida material four of the five inversions known in the right arm of the second chromosome were, however, observed, as were four of the third chromosome's fourteen inversions.

The left arms of the second chromosomes from Cuba possess a greater number of kinds of inversions than those from Florida. The fact that only one type of inversion was detected in the right arms of the second chromosome and one in the third chromosomes of the Cuban flies is not significant. Undoubtedly, the very small sample obtained from Cuba did not include all kinds of gene arrangements which occur in the Cuban population.

The number of heterozygous inversions possessed by a Drosophila fly varies from individual to individual. Da Cunha *et al.* found that some females in central Brazilian populations of *D. willistoni* possessed as many as 16 heterozygous inversions; in other regions some females had none. These investigators showed that the South American populations of this species differ from each other not only in the various kinds of inversions which they possess, but also in the mean number of heterozygous inversions per individual.

In figure 1 the mean members of heterozygous inversions per individual are graphically represented for all of the different bio-geographic regions yet studied by the various investigators. In the preparation of this figure, data for areas south of Cuba were obtained from da Cunha *et al.* (1950), da Cunha (unpublished), and Dobzhansky (unpublished). The diameters of the black circles in the figure are proportional to the mean numbers of heterozygous inversions found per individual fly in the different regions. From this figure the reader may readily determine the relative magnitudes and the geographic distribution of these means.

The mean numbers of heterozygous inversions per individual in the Florida and Cuban populations are presented in table 2. For comparison purposes selected data from da Cunha *et al.* and da Cunha (un-

TABLE 2. *Mean numbers of heterozygous inversions per individual* Drosophila willistoni. *(Data for Argentina and Salvador, Brazil, from da Cunha (unpublished); other Brazilian data from da Cunha, Burla, and Dobzhansky, 1950)*

Region[1]		Mean[2]	Range
1. Florida	♀	2.06±0.16	0–5
	♂	1.88±0.19	0–5
	♀+♂	1.99±0.12	0–5
2. Cuba	♀+♂	1.50±0.31	0–3
11. Marajó Island, Brazil	♀	2.05±0.48	0–7
	♂	0.93±0.43	0–5
16. Monjolinho, Goyaz, Brazil	♀	9.36±0.26	2–14
	♂	6.56±0.31	2–10
17. Catuní, Bahía, Brazil	♀	0.81±0.03	0–5
	♂	0.42±0.05	0–2
18. Salvador, Bahía, Brazil	♀	1.06±0.09	
	♂	0.35±0.10	
26. Rio Grande do Sul, Brazil	♀	1.90±0.24	0–4
	♂	1.25±0.42	0–3
29. Tigre, Argentina	♀+♂	1.93±0.17	
30. Buenos Aires, Argentina	♀+♂	2.28±0.19	

[1] Numbering of regions corresponds to numbering in figure 1.

[2] X-chromosome inversions are excluded from ♀+♂ means.

published) are also included in this table. Each locality listed in the table is, for identification purposes, given the same number that it has in figure 1. Where the means are presented for both sexes combined, X-chromosome inversions are excluded.

The greatest mean number of heterozygous inversions per individual has been found near Monjolinho, state of Goyaz, Brazil. The means for the Monjolinho populations do not differ significantly from those of other nearby populations. These means far exceed any for populations near the northern or southern margins of the species distribution area. All populations for which the means have been found to be lower than in Florida or Cuba are also listed in table 2. Such populations occur near the southern limit of the distribution area and at three localities in northern Brazil. The mean numbers of heterozygous inversions per individual in the populations near the southern limits of the species distribution are of about the same magnitudes as the means for the Florida and Cuban populations.

For the Florida population the mean frequencies of heterozygous autosomal inversions per individual are 2.04 $\pm$0.16 for females and 1.88 $\pm$0.19 for males. There is no statistically significant difference between these means ($t = 0.62$, with 102 degrees of freedom).

The Analysis of Concealed Genic Variability

Most mutant genes are deleterious to their carriers, at least in the environments in which the species normally lives. Dominant mutants seldom survive the rigors of natural selection for many generations. Recessive and nearly recessive mutants can persist for many generations concealed in the heterozygous condition. Populations of sexually reproducing species contain large stores of concealed genic variability. This type of variability may be studied after first rendering chromosomes homozygous. In this fashion Florida and Cuban second and third chromosomes were analyzed for their recessive effects on viability and fertility and for their contents of mutant genes producing visible effects in adult flies.

The techniques used to detect concealed genic variability were those described by Pavan *et al.* (1951). For analysis of the second chromosomes, wild males or sons of wild females were crossed in individual cultures with stock females homozygous for the second chromosome recessives *abb bw*. Single F_1 males from each culture were then bred to females which were heterozygous for a second chromosome containing *S Hk abb bw Inv 207*. This marker chromosome permits no detectable crossing over between *S* and *bw* and is lethal when homozygous. From the F_2 of each culture, virgin females and males, all showing *S* and *Hk* but not *abb bw*, were selected and inbred. For this cross about 10–15 virgin females and a like number of males were used to establish each culture in the analysis of the Florida sample. About 5–6 females and an equal number of males were used in the analysis of the Cuban material. In both analyses successive transfers without etherization were made at intervals of 3–5 days, usually 4 days, in order to produce 1–2 duplicates of each culture.

In any one culture the flies selected from the F_2 and then inbred were heterozygous for a single wild second chromosome. Their other second chromosome was the *S Hk abb bw Inv 207* one. Due to the homozygous lethal effect of the marker chromosome, the F_3 was expected to consist of two classes of flies, those showing *S Hk* and those homozygous for wild second chromosomes, in a 2:1 ratio, provided that the wild chromosome was of normal viability. When a deviation from the expected ratio occurred, it indicated that the wild second chromosome possessed mutant genes that modified viability when homozygous. The F_3 progenies were classified for mutant characters. If the cultures were not exhausted earlier, 3–4 counts of each culture were made during a period of about 12 days after eclosion

of the first adult flies from the pupae. Counts of replicate cultures were added together for statistical purposes. The cultures counted were kept at 25° C.

The technique used for analysis of the third chromosome for concealed genic variability differed from that used for the second in that third chromosome marker stocks were used in order to assure homozygosis of a single wild third chromosome in each F_3 culture. In the successive crosses the markers used were *p* and Δ *p Inv 133* (see Pavan *et al.*, 1951). The Δ *p Inv 133* chromosome reduces the recombination in the third chromosome to 0.68 per cent and is lethal when homozygous. For the Florida sample about 10 virgin females and an equal number of males, both showing Δ but not *p*, were chosen from the F_2 of each cross and inbred. Only 5–6 females and the same number of males were used for this type of cross in analysing the Cuban material. The F_3 expectancy is 2 Δ: 1 homozygote for the wild chromosome. This generation was handled in the same manner as that described above for the second chromosome.

For the Florida sample the F_3 flies in most crosses averaged between 200 and 320 per culture, rarely below 180 or above 360. Most total counts for each Florida second or third chromosome were between 400 and 850, seldom less than 200 or more than 1,000. Since only about one-half as many F_2 flies were used as parents of the F_3 in the analysis of the Cuban population, a smaller number of F_3 flies was obtained.

Controls for both the second and third chromosomes were made by crossing F_2 virgin females from one randomly chosen Florida culture with unrelated F_2 males from another Florida culture chosen at random. Several different such crosses were made. The F_3 flies resulting from these crosses were heterozygous for two different wild chromosomes, these being either second or third chromosomes according to the cultures from which the F_2 flies were taken. The same numbers of females and males used in the corresponding homozygosis tests were used in the control crosses and the cultures treated in the same manner until counting was completed.

The controls for the second chromosome yielded 37.83 ±0.82 per cent wild-type flies out of 3,534 flies counted. When compared with the expectancy of 33.33 per cent, this gives a highly significant X^2 value of 32.24. Thus, marked second chromosomes in the F_3 substantially reduced the viability of their heterozygous carriers. The marked third chromosomes, however, produced no appreciable effects on the viability of F_3 heterozygotes. Of the 6,470 flies counted in the third chromosome controls, 34.37 ±0.59 per cent were wild-type. X^2 is 3.17, which is not statistically significant.

Lethals and Semilethals

In analysing the viability effects of homozygous wild chromosomes, it is necessary to have standards of normal viability. Since marked second chromosomes in the F_3 significantly reduced the viability of their heterozygous carriers, the 2:1 expectancy was adjusted. In the analysis of the Florida and Cuban samples, this was done by taking the average percentage of wild-type flies in the F_3 of the second chromosome control cultures as the standard of normal viability of homozygotes for wild second chromosomes. Since marked third chromosomes insignificantly affected the viability of heterozygotes in the F_3, 33.33 per cent was used as the standard of normal viability of wild third chromosome homozygotes.

Although lethal chromosomes produce no viable offspring when homozygous, some F_3 cultures in the tests contained only one or two wild-type flies. For this reason, it was convenient to follow the convention of Pavan *et al.* (1951) in scoring as lethal those chromosomes which, when homozygous, reduced viability to less than 5 per cent of normal. Those chromosomes, which resulted in a viability of less than 50 per cent, but greater than

5 per cent, of normal when homozygous, were counted as semilethal.

By dividing the percentage of wild-type flies produced in the F_3 of a second chromosome test cross by the average percentage (37.83 per cent) of wild-type flies produced in the F_3 of the second chromosome control crosses, the viability effect of the test chromosome was expressed in percentage of the normal viability. The percentages of normal viability for the third chromosomes were similarly obtained by dividing the percentage of wild-type flies produced in each F_3 culture by 33.33 per cent.

The data for viability tests of the Florida and Cuban autosomes are summarized in table 3. This table also includes results obtained by Pavan *et al.* in their analysis of Brazilian *D. willistoni*. In the Florida and Brazilian material the greatest number of tested chromosomes fall into classes giving viabilities between 80 and 100 per cent. Chromosomes which are lethal or nearly lethal (0 to 5 per cent of normal viability) form the next commonest class. Chromosomes producing viabilities of 5 to 50 per cent of normal are relatively rare. The distribution of the Cuban third chromosomes differs by the relatively larger number producing viabilities greater than 100 per cent of normal. The presence of such a large proportion of these supervital chromosomes in the Cuban data is probably due in part to the application of the Florida third chromosome standard of normality and in part to sampling error because of the smaller number of flies counted in each Cuban cross; therefore, the viabilities of most Cuban third chromosomes included in the supervital classes probably do not differ significantly from the normal standard.

TABLE 3. *Viability of individuals homozygous for autosomes from Florida, Cuba, and Brazil, expressed in per cent of normal (normal viability = 100); the figures indicate numbers of chromosomes found in various viability classes. (Brazilian data from Pavan et al., 1951)*

Per cent normal viability	Second chromosome			Third chromosome		
	Florida	Cuba	Brazil	Florida	Cuba	Brazil
0	19	8	394	8	6	140
5	7		179	17	2	90
10			37	4	1	33
15	3		27	2		18
20	1		20			15
25			21			10
30			24	4		13
35	1		33	2	1	14
40		1	31	1		13
45	3		28	1		7
50			32	1		21
55	1		31			17
60	5		30		2	13
65	1	1	48			29
70	1		55	4		16
75	5	2	87	1		52
80	5		112	5	1	41
85	9	2	143	3	3	74
90	16	1	171	13		125
95	13	2	182	13	3	169
100	8	5	124	25	5	131
105	7	1	76	13	2	69
110	4	1	42	3	5	37
115			44	1	4	13
120		1	16	1	3	4
125			10		1	2
130			7			
Total	109	25	2,004	122	39	1,166

Table 4 summarizes the frequencies of lethal and semilethal second and third chromosomes of the Florida and Cuban populations. In this table the mean frequencies for Brazilian populations investigated by Pavan *et al.* and for populations studied in the southern state of Rio Grande do Sul, Brazil, by A. R. Cordeiro (unpublished) are also presented.

The upper and lower limits of the frequency range of lethal second chromosomes given in table 4 were obtained in material from southern Brazil. The upper and lower limits of the other second chromosome viability classes were secured in equatorial and southern Brazil, respectively. The frequencies of Florida second chromosomes in these classes all fall near the lower limits of the corresponding viability classes in the Brazilian populations studied by Pavan *et al.* These authors did not report any population containing as small a proportion of the lethal and semilethal class of second chromosomes as does the Florida population. In fact, the Florida

TABLE 4. *Frequencies (per cent) of second and third chromosomes with different viability effects in homozygous condition. (Rio Grande do Sul, Brazil, data from Cordeiro (unpublished); other Brazilian data from Pavan et al., 1951)*

Chromosome	Region	Lethals	Semilethals	Lethals and semilethals	Chromosomes tested
Second	Florida	23.8	7.3	31.1±4.4	109
	Cuba	32.0	4.0	36.0±9.5	25
	Rio Grande do Sul	20.2	8.2	28.4±1.8	645
	Other Brazilian	28.6	12.6	41.2±1.1	2,004
	Frequency range in Brazil	20.2–32.0	6.5–25.6	28.4–54.1	
Third	Florida	20.5	12.3	32.8±4.2	122
	Cuba	20.5	5.1	25.6±7.0	39
	Brazil	19.7	12.4	32.1±1.4	1,166
	Frequency range in Brazil	11.5–30.7	6.3–17.5	17.7–45.3	

frequency is significantly lower than the Brazilian mean frequency reported by Pavan *et al.* ($X^2 = 4.30$; for one degree of freedom this corresponds with a probability of 3.8 per cent). Cordeiro, however, recently found a slightly, but not significantly, smaller proportion of this class in Rio Grande do Sul than is herein reported from Florida. There is no statistically significant difference between the second chromosome lethal and semilethal classes of Florida and Cuba.

For each of the third chromosome viability categories, there is almost no difference between the frequencies from Brazil and Florida. The lower limits of the frequency range of the combined lethal and semilethal class and of the lethal class of third chromosomes were secured from southern Brazilian populations, while the upper limits of these classes were obtained in material from the state of Bahía. However, both upper and lower limits for semilethal third chromosomes represent frequencies for southern Brazilian populations. The Cuban frequencies of lethal and semilethal third chromosomes do not differ significantly from those of Florida.

STERILITY

Most wild chromosomes which produced viable homozygotes were tested for their effects on fertility. On the average, surviving homozygotes for semilethal chromosomes do not differ in fertility from homozygotes for chromosomes of more viable classes. Individuals homozygous for extreme semilethal chromosomes were nevertheless usually so rare in the cultures that no attempt was made to determine whether they were fertile or not. Wild-type flies from the F_3 cultures were used for fertility tests. The sexes were separately outcrossed to unrelated fertile individuals of the opposite sex. These crosses were made in creamers and kept at 25° C. If no progenies appeared within 5 to 10 days, the flies were transferred to fresh food. The second creamers were examined about one week after the transfers were made. If no offspring were produced, the sex being tested was recorded as sterile.

The data on sterility of homozygotes for Florida and Cuban second and third chromosomes are summarized in table 5. This table also presents the Brazilian mean frequency data of Pavan *et al.* (1951). In their paper these authors recorded as "sterile" any chromosome which, when homozygotes with male homozygotes from the same F_3 culture; some other tests were made by confining virgin female homozygotes with male homozygotes from the same F_3 culture; some other tests were made separately for females and for males, in a manner similar to that outlined above. The proportions of the tests

TABLE 5. *Frequencies (per cent) of wild second and third chromosomes that cause sterility when homozygous. (Brazilian data based on Pavan et al., 1951)*

Region	Sterile sex	Second chromosome		Third chromosome	
		Frequency	Number tested	Frequency	Number tested
Florida	♀ only	1.3	79	2.1	94
	♂ only	62.0	79	7.4	94
	Both	8.9	79	0.0	94
	One or both	72.2	79	9.5	94
Cuba	♀ only	0.0	17	3.6	28
	♂ only	76.5	17	17.9	28
	Both	23.5	17	3.6	28
	One or both	100.0	17	25.1	28
Brazil	♀ only	10.9		9.2	
	♂ only	18.4		16.5	
	Both	1.7		2.0	
	One or both	31.0	928	27.7	819

that were made by separate testing of the sexes were not given. However, the actual numbers of second and third chromosomes tested separately in females and in males were reported with breakdowns to show how many of these chromosomes affected each sex and how many, both sexes. For inclusion in table 5, the Brazilian mean frequencies of second and third chromosomes which, when homozygous, produced sterility in females, in males, and in both sexes were separately estimated. The calculations were made on the assumption that the chromosomes tested separately in females and males represented a random sample of Brazilian second and third chromosomes. Thus, it was assumed that, among the chromosomes tested separately in each sex, the frequencies of second and third chromosomes causing sterility in one or both sexes were equal to the Brazilian mean frequencies of, respectively, second and third chromosomes which Pavan *et al.* recorded as "sterile." Although this assumption is probably inexact, it is not likely that the estimated frequencies differ greatly from the actual ones.

All of the seventeen Cuban second chromosomes analyzed produced sterility in one or both sexes when homozygous. Furthermore, 72.2 ±5.0 per cent of the Florida second chromosomes gave the same results. These frequencies greatly exceed the mean frequency of 31.0 ±1.5 per cent Pavan *et al.* reported for Brazilian populations. Moreover, these investigators found that the frequency of wild second chromosomes producing sterility in one or both sexes was greater than 36.8 per cent in only a small sample of 14 second chromosomes from one of nine Brazilian bioclimatic regions from which populations were studied. However, the data summarized in table 5 make it quite evident that the magnitudes of the Florida and Cuban frequencies of second chromosomes producing sterility in one or both sexes are due to the exceptionally high proportions of second chromosomes which produce sterile males. It may be noted that more than three times as many Florida wild second chromosomes as Brazilian ones induce sterility in homozygous males. All of the second chromosomes tested from the small Cuban sample caused male sterility.

If one re-examines the procedures by which the flies were rendered homozygous for the wild second or third chromosomes, it may be seen that the F_3 flies in these experiments always possessed only stock X-chromosomes. This is because the single F_1 male chosen from each culture and outcrossed to marked females received his X-chromosome from his stock mother. All other X-chromosomes in the F_2 were introduced by the stock females to which the F_1 males were bred. When the F_2 flies were inbred, the F_3 inherited only stock X-chromosomes. The marker stocks used in the analyses originated from strains of *D. willistoni* trapped in Belém, state of Pará, Brazil (Spassky and Dobzhansky, 1950). Therefore, all of the flies tested for sterility effects of Florida or Cuban homozygous autosomes possessed X-chromosomes from Brazil only. These facts suggest that the high frequencies of male

sterile second chromosomes in the fertility tests may be explained by interaction of most Florida or Cuban homozygous second chromosomes with hemizygous X-chromosomes from Brazil. Unfortunately, no critical test of this hypothesis was made.

In each sterility class the frequency of Florida third chromosomes is lower than the mean frequency of Brazilian third chromosomes. The Cuban third chromosome sterility classes are intermediate in magnitude between the corresponding Florida and Brazilian classes. For the frequency of Cuban third chromosomes which, when homozygous, produce sterility in one or both sexes (25.1 ±8.2 per cent), the standard error is so large that the statistic is not a very useful measurement.

Visible Mutants

No dominant mutants affecting visible characters were discovered in either the Florida or Cuban populations. When homozygosis of the second and third chromosomes was produced in the viability tests, a number of such recessive mutants was discovered. The Brazilian data of Pavan *et al.* (1951), as well as the Florida and Cuban data, are summarized in table 6. Visible effects are often concomitant with homozygosis of extreme semilethal chromosomes. Extreme semilethals consequently were not included in counts of visible mutants.

The frequencies of total numbers of visible recessive mutants in the Florida second and third chromosomes are slightly, but not significantly, lower than in the corresponding Brazilian chromosomes. For both chromosomes, relatively lower frequencies of fully penetrant mutant genes were found for the Florida population than for Brazilian populations. In tests of Cuban flies, two recessive visible mutants were detected, both in second chromosomes.

Discussion

Two types of genetic variability were found in the Florida and Cuban populations of *D. willistoni*: first, chromosomal variants due to inversion of blocks of genes; and, secondly, recessive mutant genes carried concealed in the heterozygous condition. The biological significance of these two types of variability is quite different. Chromosomal polymorphism has been shown to be adaptive and balanced in every Drosophila species examined in this respect—namely, *D. pseudoobscura* (Wright and Dobzhansky, 1946; Dobzhansky and Levene, 1948), *D. persimilis* (Spiess, 1950), and *D. robusta* (Levitan, 1951). Although the adaptive values of the chromosomal inversions in *D. willistoni* have not been studied experimentally, da Cunha, Burla, and Dobzhansky (1950) have adduced arguments which make it virtually certain that the chromosomal polymorphism in this species is also balanced. On the other hand, the genes, or complexes of genes, which produce recessive adverse effects on viability and fertility, and visible mutants found heterozygous in many wild individuals do not clearly perform an adaptive function. This statement is not intended to mean that these genetic variants are completely recessive and that their presence in heterozygous condition does not affect the

Table 6. *Frequencies (per cent) of recessive mutants affecting visible characters when homozygous. (Brazilian data from Pavan et al., 1951)*

	Second chromosome				Third chromosome			
Region	Full penetrance	Incomplete penetrance	Total	Number tested	Full penetrance	Incomplete penetrance	Total	Number tested
Florida	5.0	8.9	13.9±3.9	79	4.3	7.4	11.7±3.3	94
Cuba	0.0	0.0	0.0	17	3.3	3.3	6.6±4.6	30
Brazil	7.4	8.5	15.9±2.2	270	8.0	8.1	16.1±1.7	477

adaptive values of their carriers; on the contrary, the data of Cordeiro (1952) prove that at least some of the lethals found in natural populations have slight, but perceptible, dominant effects. There is not yet, however, any evidence that the heterozygosis for lethals and other concealed variants is involved in adaptation of the populations to their environments. Such heterozygosis is rather the result of mutation pressures which inevitably produce some recessive variants that are not eliminated at once by natural selection. The rate of elimination of genes which may form recessive deleterious gene complexes will, of course, also be a function of the rate at which such complexes are produced by crossing-over.

Da Cunha *et al.* have put forward a hypothesis according to which the variety of chromosomal types present in a population is positively correlated with the diversity of ecological niches which this population has been able to master in a given territory. This hypothesis is a modern version of Vavilov's (1926; 1951) theory of "centers of origin," according to which the highest diversity of genetic types should be found in the territory which has been settled by the species for the longest time. Da Cunha *et al.* have argued that the extent of the adaptive polymorphism should decrease from the center of origin towards the periphery of the species distribution. At the margins of the distribution area, the species is prevented from expanding its range because it has not had time to evolve adaptive polymorphism sufficient to permit control of many local environments and enable it to spread further. (This assumes, of course, the absence of impenetrable geographic barriers which forbid the expansion of the territory.) Marginal populations are thus expected to contain less adaptive polymorphism than do the populations of the central areas.

Elton (1950) has defined the ecological niche of an animal as "the mode of life, and especially the mode of feeding." The ecological niche concept, as applied to Drosophila, includes both the food niche and habitat niche concepts of Allee *et al.* (1949).

Dobzhansky and Pavan (1950) have shown that in the equatorial forests of Brazil *D. willistoni* is widespread, usually more abundant than elsewhere, most often the commonest species of Drosophila, and the occupant of a greater variety of habitats than is any other Drosophila species. *D. willistoni* is known to feed on a large variety of tropical fruits. Da Cunha *et al.* have pointed out that, while it is at present impossible to enumerate ecological niches, it is nevertheless possible to conclude that a fruit-feeder has more ecological niches available to it in a region with a varied fruit-bearing flora than in a region with a limited and less varied fruit-bearing flora. Black, Dobzhansky, and Pavan (1950) have shown the strikingly large amount of diversity and great density of trees, including fruit-bearing species, in Brazilian rainforests. The variety and density far exceeds that in Cuba, where forests have been permitted to remain in only a few small areas, and that in Florida, where most tropical fruits are borne by introduced species. Ecological niches similar to those controlled in equatorial Brazil by *D. willistoni* are thus considerably limited in Florida and Cuba. If the hypothesis of da Cunha *et al.* is correct, it would therefore be expected that the Florida and Cuban populations of this species possess less chromosomal polymorphism than do the populations living near the center of the species distribution.

The data presented in this paper are in general agreement with the hypothesis of da Cunha *et al.* In certain populations of central Brazil, a female of *D. willistoni* is heterozygous on the average for 9.36 $\pm$0.26 and a male for 6.56 $\pm$0.31 inversions. Figure 1 shows that, proceeding from central Brazil towards the periphery of the species distribution in Florida and Argentina, there is generally a decrease in the mean number of heterozygous inversions per individual. Exceptionally low frequencies have been found in northern Brazilian populations (da Cunha *et al.*,

1950; da Cunha, unpublished) from: Marajó Island (11); Catuní, Bahía (17); and Salvador, Bahía (18). The females of Catuní possess 0.81 ±0.03 heterozygous inversions per individual, and the males of Salvador 0.35 ±0.10 per individual. These are the lowest frequencies yet recorded for the respective sexes. Da Cunha *et al.*, who reported the Marajó Island and Catuní frequencies, explained that the Bahía "caatinga" deserts are ecologically close to the limit of tolerance for *D. willistoni* and do not support large populations of this species. Furthermore, these investigators found the composition of the Drosophila fauna to be atypical on Marajó Island and in Belém (12), where *willistoni*-like species are rare and *D. willistoni* is not the dominant member of this group. The frequency of heterozygous inversions per individual, ♀ + ♂ 1.99 ±0.12, in the Florida population is about the same magnitude as those found (da Cunha, unpublished) for populations from Argentina, ♀ + ♂ 1.93 ±0.17 and ♀ + ♂ 2.28 ±0.19, respectively, from Tigre (29) and Buenos Aires (30).

Qualitative comparison of the inversions found in Florida with those found elsewhere is also interesting. Of the 11 kinds of inversions recorded in Florida, only one, *A–1* in the third chromosome, has not been discovered in Brazilian populations. In fact, most of the inversions that occur in Florida occur also in the far-flung territory southward from there, at least as far as southern Brazil. On the other hand, many kinds of inversions known in Brazil do not seem to have reached Florida. Even in the very small Cuban sample studied, some inversions not found in Florida were recorded (*XL–D and IIL–F*). While this apparent absence in Florida may be spurious, it is quite possible that these inversions have not yet reached the marginal Florida population although they have settled Cuba. The Florida population contains therefore only about one-quarter of the kinds (41) of inversions known in *D. willistoni*, whereas some central Brazilian populations of this species contain two and even three times as many as does the Florida population.

Here it must be mentioned that the presence of similar inversions in populations as remote as Florida, central Brazil, and southern Brazil is in itself noteworthy. Dobzhansky (1944; 1951) has shown that all the chromosomes with a given gene arrangement in the species are probably descended from a single progenitor in which the arrangement resulted from a chromosomal mutation. The reason for this view is not only that a repeated origin of the same inversion in nature must be a rare event, but also that an inversion is not likely to be retained or to increase in frequency in a natural population unless it happens to include a gene complex which has a high adaptive value when heterozygous with other gene complexes in the same population. While the huge number of individuals in the species *D. willistoni* may enable rare events to occur repeatedly, even in this highly variable species the number of kinds of inversions which happened to arise in chromosomes with favorable gene complexes is limited. It is then indeed unlikely that any one gene arrangement would arise two or more times in chromosomes which contained heterotic gene complexes. Thus, the occurrence of a particular gene arrangement in extensive territories indicates both an efficient mechanism of diffusion of selectively valuable traits through the species population and a relative antiquity of the arrangement. Assuming that such widespread gene arrangements first appeared somewhere near the present center of the species distribution area, in the equatorial part of South America, they had to overcome a distance of at least 3,000 miles to reach Florida.

Unfortunately, the method used to analyze the populations for concealed genic variability did not distinguish whether a recessive mutant effect was due to homozygosis of a single gene or to homozygosis of several mutant genes in the tested chromosome, or whether the recessive effect would have resulted if the chromosome had been rendered homozygous in

some other genetic background. Nevertheless, the method does provide valid indices for comparison of the relative magnitudes of stores of concealed genic variability in different populations of the species.

The incidence of chromosomes producing recessive mutant effects is far more uniform throughout the species range than that of chromosomal polymorphism. The frequencies of lethal and semilethal second and third chromosomes in Florida populations are 31.1 ±4.4 per cent and 32.8 ±4.2 per cent, respectively. The mean frequency for Brazilian populations studied by Pavan *et al.* (1951) is 41.2 ±1.1 per cent for the second and 32.1 ±1.4 per cent for the third chromosomes. The figure for the second chromosome is significantly higher for the Brazilian populations than for the Florida one. It should, however, be noted that the frequencies of lethal and semilethal chromosomes are not uniform in populations from different regions of Brazil. The Florida population's frequency of lethal and semilethal second chromosomes does not differ significantly from 28.4 ±1.8 per cent which Cordeiro (unpublished) has found for populations in Rio Grande do Sul, Brazil, close to the southernmost known limit of the distribution area of the species.

Third chromosomes which, when homozygous, produce sterility in one or both sexes are significantly less frequent in Florida than in Brazil, 9.5 ±3.0 per cent and 27.7 ±1.6 per cent, respectively. In fact, the frequency of Florida third chromosomes of this class is lower than the lowest frequency (13.7 per cent) Pavan *et al.* reported for any Brazilian population. In tests with Brazilian marker stocks, the Florida second chromosomes effected sterility in one or both sexes 72.2 ±5.0 per cent of the time. This is very significantly higher than the frequency of 31.0 ±1.5 per cent Pavan *et al.* reported for Brazilian populations. At present, however, it is impossible to rule out the hypothesis that the Florida second chromosome sterility frequency is in large part due to interaction of the Brazilian X-chromosome and the homozygous Florida second chromosomes in many of the males tested.

Detection of mutants affecting visible characters is an operation that requires observational skill, a talent which may be much better developed in some investigators than in others. The frequencies of recessive visible mutants in Florida populations of *D. willistoni* reported herein and those Pavan *et al.* (1951) recorded for Brazilian populations are therefore not strictly comparable. Nevertheless, the lower frequencies, 13.9 ±3.9 per cent and 11.7 ±3.3 per cent, respectively, for the second and third chromosomes, in the Florida population do not differ significantly from the Brazilian frequencies of 15.9 ±2.2 per cent for the second chromosome and 16.1 ±1.7 per cent for the third chromosome.

It appears then that the marginal populations of the species, both at the northern and southern boundaries, have somewhat lower frequencies of autosomes producing recessive adverse effects on viability and fertility (in northern marginal areas the low incidence of sterility factors is certain only for the third chromosome), and, possibly, possess fewer recessive visible mutants than do populations near the center of the distribution of the species. Now, the magnitude of the store of concealed recessive variants carried in a population depends upon the interaction of several factors (Wright, Dobzhansky, and Hovanitz, 1942), perhaps the simplest of which is the mutation rate that produces the recessive variants. Thus, in an effectively infinite population, the equilibrium frequency of a completely recessive autosomal lethal is equal to the square root of the frequency of *de novo* origin of that lethal by mutation. Variations of the mutation rates in different populations of a species have been found both in *D. melanogaster* (Ives, 1945; Dubinin, 1946) and in *D. willistoni* (Dobzhansky, Spassky, and Spassky, in press). Unfortunately, no data which would permit comparison of the mutation

rates in the Florida and in the Brazilian populations are available.

Apart from the mutation rate, the reproductive biology of a population also influences the frequencies of concealed recessive variants. As shown especially by Wright, the equilibrium frequencies of lethals and other deleterious variants are lower in effectively small populations than in effectively large ones. This seems to be the probable explanation of the differences between frequencies of chromosomes having recessive lethal effects found in *D. melanogaster* populations of the United States by Ives (1945), of Russia by Dubinin (1946), and of Israel by Goldschmidt (1951). Similarly, Wright, Dobzhansky, and Hovanitz (1942) found that the effectively smaller populations of *D. pseudoobscura* in California have fewer chromosomes producing recessive lethal and semilethal effects than the effectively larger populations which inhabit Mexico and Guatemala. Somewhat lower frequencies of deleterious variants may therefore be expected in marginal populations of a species than in those near the center of the distribution area.

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Summary

Samples of marginal populations of *D. willistoni* from Florida and Cuba were analyzed for chromosomal and genic variability. All of the inversions found in these populations have, with a single exception, previously been reported from central and southern Brazil. The Florida population nevertheless possesses only about one-fourth of the known kinds of inversions. The Florida and Cuban mean frequencies of heterozygous inversions per individual fly are much lower than those in populations which live near the center of the distribution area of the species. However, similar frequencies of heterozygous inversions have been found in marginal poulations in Rio Grande do Sul, Brazil, and in Argentina. Chromosomes containing the different types of concealed recessive mutants are, in general, somewhat less frequent in Florida and Cuba than in central Brazil, but about as frequent as in Rio Grande do Sul, Brazil.

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NOTES AND COMMENTS

SEX DETERMINATION IN THE HONEY BEE

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Recently Sanderson and Hall (1951) have criticized the observations of Kerr (1951) and Manning (1949–50) concerning evidence for the existence of a sex chromosome in the honey bee. The criticism, however, makes curious reading in view of the fact that these authors (1948) were unable to demonstrate even cytoplasmic buds in the spermatocytes of this insect. Since the latter often approach 1/8 size of a normal cell we may justifiably question the adequacy of the techniques used by them.

However, the main contention in the article under review is that Kerr's observations do not support Manning's; first, because the extruded body is a naked mass, and, second, because Kerr has accepted Manning's evidence on differential maturation of the egg which *"is unsatisfactory and far from complete."* Such sweeping statements are very misleading. Surely, the extrusion of a chromosome from within an established spindle does not entail envelopment within a nuclear membrane. The latter, indeed, will form either at the dissolution of the spindle, or when the extruded body has reached the periphery of this structure. Since, in the honey bee, both occur at the same time it is not surprising to witness the formation of a very small daughter cell of the kind postulated by Sanderson and Hall simultaneously with the re-formation of the main nuclear membrane. Unfortunately, the smallness of the cell and its late appearance have led investigators to ignore it. In the bumble bee where the extrusion of the differential chromosome is now known to be similar to that of the honey bee (Manning, in the press), the nuclear membrane is larger and thus the daughter cell more distinct.*

The second of Sanderson's and Hall's contentions apparently partly hinges on the fact that Manning omitted the reproduction of illustrations of an oogonial plate to support his oogonial counts (Sanderson and Hall, 1951). Oogonial chromosomes, however, are very small and though counts are readily made, the production of indisputable photocopies is very difficult and has not yet been accomplished (cf. figure 2, p. 35, Endeavour, 1951). Thus for publication it seemed better to commit the sin of omission rather than that of commission, particularly since the chromosomes in any case were figured. It will be noticed, too, that in this matter Sanderson and Hall are in a very strong position to exploit the situation, since they need only produce satisfactory evidence for the presence of *two* hooked-chromosomes to bring devastating proof against the accuracy of Manning's observations and thus demonstrate the sincerity of their criticism.

As far as incompleteness of the study of oogenesis is concerned, this is frankly admitted. Such work is very slow and tedious as most investigators appreciate. Nevertheless, even in the early paper far more work had been done than Sanderson and Hall recognize and since then considerable progress has been made, so that soon many old and new facts will be published in support of earlier statements.

Finally, it is amazing still to find the promulgation of the belief that sex determination depends on "haplo-diploidy." Surely, the latter is no more than a term descriptive of the state of two genomes and cannot be applied as a fundamental theory. If Sanderson and Hall find published work unsatisfactory (and readers must judge this) surely we might expect from them a clarification of the ideas they are supporting, and not a resort to mere descriptive terms, or an equivocal statement about the presence of a sex chromosome which, if its existence is admitted, can at least balance the autosomes for the determination of sex in the honey bee.

* In vespoid wasps the phenomenon is even clearer due to the formation of a supplementary spindle for the differential chromosome(s), prior to the formation of nuclear membranes.

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SEX DETERMINATION IN THE HONEY-BEE

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The cytology of the honey-bee has been frequently investigated during recent decades (for lit. see Kerr, 1951). While a number of questions remain it is generally agreed that the males develop from unfertilized eggs and contain 16 chromosomes, the haploid number, except where polysomaty has increased it secondarily. The first spermatocyte division is suppressed so that no chromosome reduction occurs and the sperms carry 16 chromosomes. Females, on the other hand, originating from fertilized eggs are diploid with 32 chromosomes. Recently this view was challenged by Manning (1948–1950), who claimed that he had discovered "A hitherto unsuspected x-chromosome" and who proposed a new scheme of sex determination for the honey-bee, based on a balance between the number of autosomes and x-chromosomes. According to Manning the large hook-shaped chromosome that is found among the 16 chromosomes of spermatocytes is eliminated in the second spermatocyte division. The sperms therefore could contain only the 15 autosomes resulting in a basic number of 31 in females, 30 autosomes and one large hook-shaped x-chromosome. Kerr (1951) published some observations that appeared to confirm Manning's story of the elimination of the x-chromosomes during spermatogenesis. He found a double body that clearly lagged behind in the second spermatocyte anaphase and was not included in the daughter nuclei.

Neither Manning nor Kerr, however, had used the Feulgen reaction, or had definitely proven that the eliminated body was indeed a chromosome.

Since such an x-chromosome, if substantiated, would radically change the present ideas on sex-determination in the honey-bee (Mackensen, 1951) we undertook to re-investigate the spermatogenesis, using the Feulgen reaction in squashes and sections as well as iron-hematoxylin. The material used includes all the different stocks we could obtain, namely English, Italian, Caucasian * and a Brazilian stock originally studied by Kerr.

The present investigations confirm the previous work of Manning and Kerr, insofar as (in all stocks studied) after iron hematoxylin staining, a sometimes double body is found lagging in the spindle of the second meiotic division, and is finally eliminated from the nucleus (fig. 1). However, it turned out that this body is not a chromosome. Never is it even slightly Feulgen positive (fig. 2) and in preparations counterstained with fast green it stains clearly green. In the second spermatocyte metaphase it is always apart from the chromosomes and nearer to one pole (fig. 3). Yet the metaphase plate shows 16 Feulgen positive chromosomes including the large hook-shaped one. The body eliminated is therefore not the large chromosome as Manning claims.

Our findings support the results of the older investigators that spermatocytes contain 16 chromosomes that divide once equationally and

* We wish to thank Mr. W. C. Roberts of the U.S.D.A. in Madison, Wisconsin, for the material and the help in collecting it.

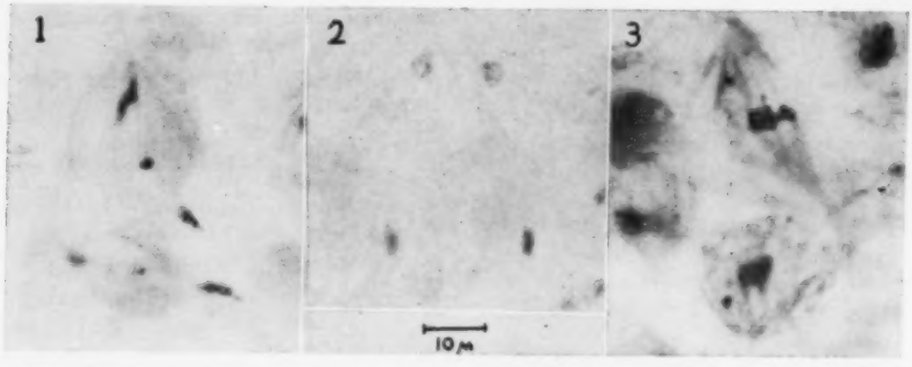

FIG. 1. Second spermatocyte telophase of *Apis mellifera* L. (Brazilian stock) stained with Heidenhain's iron hematoxylin. Note the structure lagging in the spindle.

FIG. 2. Second spermatocyte telophase, Feulgen. No lagging body is visible here.

FIG. 3. Second spermatocyte metaphase, iron hematoxylin. The Feulgen negative body is seen nearer to one pole.

that the sperms carry 16 chromosomes into the egg. There is no morphologically visible sex chromosome in the honey-bee.

What is this lagging body, if not a chromosome? The history of it as well as other puzzling aspects of spermatogenesis in the bee such as the secondary association in metaphase II are under investigation and will be published elsewhere. From preliminary studies it appears that the structure described by Manning and by Kerr is the nucleolus that persists from the prophase of the primary spermatocyte into the spermatid.

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THE EVOLUTION OF CULTIVATED PLANTS AND WEEDS

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A paradoxical situation has arisen for students of plant evolution. We have come to realize more and more clearly that rapid evolutionary change is bound up with alteration of the environment, and that the most radical and sudden changes in the environment which have taken place in recent years and are still taking place are the result of man's activity. Hence the best place for us to look for evolution in progress should be among those plants associated with man. But when we come to study such plants, we find that they have been given relatively little attention by systematic botanists and others interested in species relationships and phylogeny, and until recently geneticists have studied them mainly for obtaining information about the mechanism of heredity, and only incidentally for learning about their origin and relationships.

This situation is the main theme of a recent book by Edgar Anderson.[1] There is certainly nobody better qualified to write on such a subject. Dr. Anderson is the only living botanist, and in fact the only botanist who has ever lived, who has studied intimately the variation pattern in many groups of both wild species and cultivated plants, and at the same time has known enough about modern genetics and cytogenetics to interpret these patterns in terms of heredity. For these reasons, serious botanists and evolutionists must respect Dr. Anderson's views, even though they may disagree with them.

The present book is written in a popular, conversational style, and is obviously intended for the intelligent layman. Furthermore, it is full of intimate character sketches of botanists, from the herbalist, Leonard Fuchs, ". . . a big, broad-shouldered Henry-the-Eighth sort of man with handsome clothes and a general air of getting things done . . . ," through Harvard's austere economic botanist, Oakes Ames, who ". . . had the mind of a scholar with the soul of an artist . . . ," up to the unnamed taxonomist who on reaching a Central American cloud forest ". . . rushes about with a great excess of energy, throwing the plants into presses, searching here and there for something uncollected . . . as if somehow he is trying to make the cloud forest a part of his professional self . . . ." This characteristic will certainly help to assure a large number of readers among scientists as well as laymen. Botanists familiar with Dr. Anderson's ideas will enjoy his presentation of them and his characterization of old and new friends, both human and angiospermous. Other botanists will find this book a most pleasant way of getting acquainted with his methods as well as his ideas. Graduate students should read it, if only to learn that it is possible for a true scientist to write in a delightfully popular vein, without becoming either inaccurate or vulgar. To observant laymen, the book may open up an entire new world of interest; one which they can follow in their own gardens, and in journeys to any place, far or near. This reviewer welcomes it as ideal to recommend as reading to his intelligent non-scientific friends who wish to learn what he is doing.

To the evolutionist, the biggest problem raised by this book is that of evaluating Dr. Anderson's methods and ideas, particularly since they will now become known to a large number of people who are neither geneticists or evolutionists. With one of them, namely, the need for learning much more about the variation pattern in both cultivated plants and weeds, nobody can quarrel. The comparative neglect of these plants on the part of systematic botanists has been due largely to the fact that the traditional methods of systematics have revealed little more about them than was known to Linnaeus and

[1] Anderson, E., Plants, Man, and Life. 245 pp., 16 figs. Little, Brown and Co., Boston, 1952.

the herbalists. Real progress in the study of such plants requires concerted attacks by systematists, geneticists, economic botanists, and agriculturists, all of whom are well enough acquainted with each other's disciplines so that they can understand each other. Such cooperative projects are outside of the scope of most herbaria and botany departments of universities, which perform many other equally important tasks dealing with native floras and plants in general. Fortunately both research workers and administrators of colleges of agriculture are realizing more and more that they can produce better crop plants more efficiently if they learn all that can be known about crop plant species and about their relatives, many of which are common weeds. As a result, cooperative studies of cultivated plants and weeds are becoming a feature of research programs in colleges of agriculture. and are becoming more and more firmly based upon fundamental principles of genetics and systematics. Many examples can be given, some of them mentioned by Dr. Anderson: the exploratory studies of Vavilov and his associates in Russia on a great variety of plants; the work of Kihara's group in Japan and of MacFadden and Sears in Missouri on wheat; that of Mangelsdorf and Reeves and of Anderson himself on maize; that of Hutchinson and Stephens and of the Texas A. & M. group, originally headed by the late Dr. Beasley, on cotton; the studies of R. E. Clausen and his associates on tobacco; and the recent cooperative work in the University of California, Purdue University, and elsewhere on the tomato. The outcome of such projects will give us a greatly increased insight into the evolution of cultivated plants and weeds.

More controversy has been aroused by Dr. Anderson's methods of research, as well as the working hypothesis which he has recently developed as a result of these methods. In considering these, however, the evolutionist should also study the most recent research publication of Dr. Anderson, in which he has clearly stated his working hypothesis, and has described his most recently refined method of charting variation in natural populations.[2]

One can hardly deny the fact that Dr. Anderson has developed ways of sampling populations and of collecting and preserving herbarium material which are far more useful to students of evolution, particularly as applied to cultivated plants, than any which existed previously. Also, it is hard to deny that Dr. Anderson's graphic representation of variation, through the use of scatter diagrams and ideographs, is very useful for certain problems. This method, which has been gradually evolved through the years and of which various modifications are described in several publications, is presented clearly in its newest and most efficient form in a chapter of the present book entitled "How to measure an avocado." This reviewer and his students have used it enough to learn that this method is by far the best yet devised for making the observer aware of a pattern of variation in respect to three or more characters which are varying simultaneously. To be sure, the selection of the characters to study and of their arrangement on the diagram are based on just as strictly subjective judgment as are the descriptions of the traditional systematist. But once the method is learned, it is, like every other good scientific method, a valuable tool for making complex natural phenomena relatively clear to the human mind, without seriously distorting them.

The numerical indices devised by Dr. Anderson, particularly the hybrid index, have been the most criticized of his methods. They have been used less and less frequently in Dr. Anderson's most recent publcatons, and are not mentioned at all in "Plants, man, and life." Perhaps the main reason for criticizing them has been their apparent mathematical objectivity, which has caused them to be compared with the much more precise methods of statisticians. Such comparisons are not justified. Dr. Anderson has never intended that they should replace statistical methods, if the data available permit the use of statistics, and if the problem concerned is one which can be solved by the statistical methods currently available. It seems to this reviewer that gathering sufficient data to permit statistical analysis of the variation pattern in even a single species is almost an impossible task. This fact has caused scientists who feel that statistical analysis is essential to confine their attention to two or three easily measured characters, and often to overlook altogether the most important characteristics which separate species, and to pay far too little attention to the interrelationships between variation in different characteristics. For a complete analysis on a sufficiently large scale of morphological variation in natural populations, statistical methods are at present an unattainable ideal. Dr. Anderson's methods, both numerical and pictorial, are frankly a compromise between this ideal and the completely subjective intuition which is the chief basis of most of the decisions made by many systematists working with traditional methods. They have the advantage of being repeatable and of focussing the attention of the observer upon certain essential features of variation. Once their limitations are recognized and they are applied correctly and with careful discrimination, they become of indispensable value to botanists interested in species relationships and evolution.

[2] Anderson, E., and Amy Gage, 1952. Introgressive hybridization in *Phlox bifida*. Amer. Jour. Bot., **39**: 399–404.

Finally, we must consider the probability of Dr. Anderson's principal working hypothesis. This is the belief that hybridization, and particularly introgression, provides one of the principal sources of the variation observed in natural populations of higher plants, as well as that possessed by cultivated species. Whether this is to be considered as hybridization between species or between subspecies depends upon the species definition employed, and is perhaps not of paramount importance. Two previously isolated subspecies which possess widely different adaptive characteristics may by hybridization produce as much or more genetic variability than results from crossing between some species, particularly those which possess very similar adaptive requirements. Furthermore, an increasing amount of evidence is pointing to the probability that very strong barriers of hybrid incompatibility or sterility which separate well isolated species can be overcome if the selective value of the hybrid derivatives is sufficiently great.

In considering this hypothesis, the first thing to recognize is that it is only an hypothesis, which will require the assembling of many facts in favor of it obtained from a variety of different plants, before it can be generally accepted. We must also recognize the fact, however, that the alternative hypothesis, namely that hybridization has not been an important factor in evolution, is a null hypothesis. This is the hardest type of hypothesis to establish firmly, and must be considered particularly subject to revision if new methods of research produce new types of evidence against it. Most systematists since the days of Linnaeus have had a strong bias against the assumption of widespread natural hybridization, partly because recognition of such a condition implies the admission that natural species are in many instances not clear cut entities, and the creation of a perfect taxonomic system is therefore an unattainable ideal. If a particular individual or population possesses key characters which place it definitely within some recognized taxonomic category, the systematist usually concludes that "it is obviously not a hybrid." But if for the word "hybrid" we substitute the phrase "of hybrid origin," then this conclusion would in most instances be more valid if it were modified to read, "It is not obviously of hybrid origin."

The principal reason for the last statement is the evidence from cytogenetics which shows clearly that populations of hybrid origin may possess few or none of the characteristics usually associated with hybrids, and may exist in regions far removed from the present distributional area of either of their original parents. These facts have long been known for polyploid derivatives of interspecific hybrids, and Dr. Anderson's recent and current work show that they are also true of back cross or introgressive derivatives of hybridization. These latter are often hardly distinguishable from typical members of the parental species, as has now been shown by a number of experiments.

The present state of the controversy concerning the importance of hybridization in evolution can best be summarized by enumerating the principal objections which have been raised against the assumption that hybridization plays a major role in evolution, and by stating the principal evidence affecting these objections.

The first objection, namely, that the proponents of hybridization have often considered entities to be hybrids which occur in regions far removed from those occupied by their putative parents, has been largely removed by cytogenetic evidence. We now realize that among the products of hybridization between species or subspecies in nature, individuals of the F_1 generation usually form a very small minority. In most instances, they are far outnumbered by F_2 or back cross types, if the hybridizing entities are closely enough related so that the F_1 can produce some progeny, or by allopolyploid derivatives, in the case of hybrids between distantly related species. Provided that these later products of hybridization find an ecological niche in which they have a selective advantage, they can perpetuate themselves indefinitely, and can spread far beyond the distributional range of either of their original parents. They may also survive long after one or both of these parents have become extinct.

A second objection is that gene recombination in the progeny of species or subspecies is so complex that inferences concerning the hybrid origin of natural populations cannot be made unless the supposed hybridization is repeated under controlled conditions. Fortunately, there are now several examples not subject to this objection, since experimental evidence is available. Two of the best of these, *Tradescantia* and *Helianthus*, are discussed in Dr. Anderson's book. In both instances predictions first made on the basis of evidence from natural populations were fully verified by experimental data. More examples of this sort are badly needed, but those available point to the likelihood that at least the majority of the inferences based upon careful studies of natural populations (but not necessarily those based on casual examinations of individual herbarium specimens) are correct. The reasons why such inferences can be made are outlined in Dr. Anderson's earlier book, Introgressive hybridization. They are based chiefly on the fact, now verified by a great mass of experimental data, that most differences between natural species

and subspecies are governed by quantitative inheritance, so that in respect to them an F_1 hybrid is intermediate between its parents, and F_2 or backcross derivatives form graded series connecting the F_1 with one or both of its parents. Furthermore various genetic forces, chiefly pleiotropic effects and linkage, can promote correlations between characters, and these correlations may be further augmented by natural selection, which is likely to sort out as units favorable character combinations which have been built up by selection during the evolutionary history of a successful species. The principal object of Dr. Anderson's methods is to enable the observer to see correlations between characters which he would otherwise overlook. Based on the detection of such correlations, Anderson has been able to predict the existence of putative parental entities unknown to him, and to find these entities by searching through floras, herbaria, or in the field. The fact that this reviewer and other botanists have been able to use Dr. Anderson's methods in the same way is the strongest possible argument for their value.

A more serious objection has been that inferences made on the basis of these methods have in some instances pointed toward hybridization between species which cannot be crossed in the laboratory, or toward the production of progeny by F_1 hybrids which under all observable conditions are completely sterile. There are several answers to this objection. The first one is that the ability to cross with another species varies widely from one population to another of any species, and even from one individual to another of the same population, so that the investigator can never hope to try all of the possibilities for crossing which have been available to two sympatric species during the thousands of years of their coexistence. Second, whereas the hybridizer must be content with experiments involving only hundreds or perhaps thousands of female gametes, nature's experiments may have involved tens or hundreds of thousands of such gametes, even during a single season. A universal experience among those hybridizing species has been that many crosses at first deemed impossible succeed after repeated efforts on a large scale. The same type of answer may be applied to the production of progeny by "sterile" hybrids. The production of progeny by a mule was long considered impossible, but is now generally recognized as having occurred at very rare intervals. In his work with grasses, the writer has encountered a number of situations which almost certainly require the production of seed by interspecific hybrids which in his garden have to date proved completely sterile. He has also found that very great differences exist in fertility between different F_1 individuals of the same hybrid progeny, to say nothing of the even greater differences between progeny from different populations of the same parental species. To say that two species "cannot be crossed" or that their F_1 hybrid "is completely sterile" in many instances implies an omniscience which is not scientifically justified.

Finally, the objection has been raised that if all variation within natural populations is due to hybridization between previously distinct entities, then how do new characters arise? One reply is that new variations are, in fact constantly occurring, but that they are overshadowed by variation due to recombination of characters belonging to previously existing variants. In morphologically constant, genetically stable populations which are well adjusted to their environments new mutations are almost certain to lower the adaptive value of their bearers, and so to become eliminated, as Dobzhansky and other geneticists have frequently observed. But when crossing between widely different types is taking place in a disturbed environment, new gene combinations are constantly being exposed to novel environmental conditions. Under such circumstances, it is entirely possible that mutations (in the broadest sense of the word) which previously were rejected repeatedly by selection may occur anew and find themselves in a genetic and environmental milieu in which they are highly successful, and so may spread rapidly soon after they have occurred. To use an analogy, hybridization may be regarded as an evolutionary catalyst. In combination with another catalytic agent, disturbance of the environment, it may promote evolutionary changes far more rapidly and to a far greater extent than is possible under any other circumstances, without being itself the direct basis of the new characteristics. At present, the evolutionist must keep his mind open in respect to this as well as many other problems, and welcome new techniques like those of Dr. Anderson, which enable us to gain new insight into it.

COMMENTS ON EVOLUTIONARY LITERATURE

ERNST MAYR

Ammonite evolution.[1] The discovery of a rich ammonite fauna in central Arabia poses several interesting problems. Within the Jurassic at least six virtually world-wide and exceedingly abundant faunas are known. Only a few representatives of a single one of these faunas have been found in the rich Arabian beds. "Instead there is a succession of peculiar and recondite ammonites which . . . at first sight might have been collected on another planet." Not only are there endemic genera, but even the non-endemic genera are elsewhere rarities or generally considered aberrant. There is reason to believe that the embayment where this fauna occurred had only tenuous contact with other oceans and might furthermore have been ecologically aberrant. The evolutionary potentialities of such a fauna are at once evident. If it is permitted to break out of its isolation owing to a change of ecological and geotectonic conditions, it may sweep the oceans. All the geologist would find at a distant locality is what Cuvier would have called a cataclysm, or what some paleontologists would call a macro-mutational succession. That different faunas can co-exist at the same time level, but in different oceans or continents, seems to be one of the most difficult things to understand for a worker specializing on a single fauna. And that a replacement of such a fauna at a given locality is a zoogeographical event and not an evolutionary event (in the narrow sense) is a fact that cannot be emphasized often enough.

There is one other aspect of this study which calls for comment. The study of ammonites is still analytical. Within each genus every morphologically different type is described as a different species. But what are these morphological "species" biologically? Take, for instance, the genus *Ermoceras* restricted to the bordertime between Middle and Upper Bajocian (Jurassic) in Arabia and Sinai. Three subgenera with ten species are distinguished morphologically. As an ignorant outsider I would like to make the iconoclastic suggestion that all these forms may be no more than individual variants and ecophenotypes of a single species! Arkell points out quite correctly (p. 305) that there were no geographical barriers within the range of *Ermoceras* that would have permitted such proliferation by geographic speciation. As an out, he takes recourse to the discredited hypothesis of ecological speciation. However, Arkell fails to adduce any proof that these different morphological types are really different and reproductively isolated populations. Anybody familiar with the ecophenotypic variation in *Melania*, *Limnaea* and *Anodonta* among the living mollusks would not be surprised at a similar situation in these champions of morphological plasticity, the ammonites.

Eocene marine faunas.[2] The conclusions that can be drawn from marine faunas are in harmony with the results obtained from the study of terrestrial faunas: the tropical belts were in the same position as now, except extending farther towards the poles. The relationship of the Paleocene-Eocene faunas of the Americas and Europe-Asia indicates that the two regions were then as far distant from each other as they are now.

Fossil birds.[3] A survey of the fossil birds described since 1932. The existing genera of birds may largely go back to the Miocene. Most of the genera known from the Eocene are placed in families or subfamilies different from the living ones.

The natural system and phylogeny.[4] Every thinking biologist is aware of the methodological and conceptual difficulties connected with the words phylogeny and natural system. The never ending arguments on the meaning of the word homology, the question whether or not the natural system should be (or can be) based on the findings of evolutionary results are indicative of the difficulties. Remane presents in the present volume a historical, philosophical and biological analysis of this complex of questions. His analysis is very thorough, over 70 pages, for instance, are devoted to a discussion of homology and analogy. Additional problems, that are discussed, are the meaning of phylogeny, polyphyletic groups, the type problem, recapitulation, manifestations of orthogenesis, shift of function, irreversibility, rudimentary organs, the interrelations between comparative anatomy and paleontology, and many others. The discussions are illustrated throughout by instructive examples from Re-

[1] Arkell, W. J. 1952. Jurassic ammonites from Jebel Tuwaiq, central Arabia. Philos. Trans. R. Soc., B (Biol. Sci.), **236**: 241–313.

[2] Durham, J. W. 1952. Early Tertiary marine faunas and continental drift. Amer. Jour. Sci., **250**: 321–343.

[3] Wetmore, A. 1951. Recent additions to our knowledge of prehistoric birds 1933–1949. Proc. Xth Int. Ornith. Congress, Uppsala, pp. 51–74.

[4] Remane, A. 1952. Die Grundlagen des natuerlichen Systems, der vergleichenden Anatomie und der Phylogenetik. Theoretische Morphologie und Systematik I. Akad. Verlagsges. Leipzig, 400 pp.

mane's matchless knowledge of invertebrates and vertebrates. The underlying thesis of all discussion is that the various vitalistic phylogenetic "laws" are based on misconceptions and are not a necessary interpretation of the observed facts.

Some of the discussion may seem superfluous to the Anglo-Saxon reader since the rejected theories cannot be reconciled anyhow with the findings of genetics. However, it must be remembered that such theories are still widely held among anatomists and paleontologists, not only in continental Europe, but occasionally also elsewhere. To show the inconsistency and general weakness of such theories on the basis of the very material on which they were founded is thus of considerable value. It is therefore irrelevant that Remane himself is not familiar with the more recent developments of genetics, as is very evident from his discussion of mutation. Every comparative anatomist, systematist and evolutionist will benefit from reading Remane's systematic analysis of this complex of questions.

Morphology and phylogeny.[5] In this review on the literature of the comparative morphology of the arthropods, a discussion of the literature is so well integrated with an independent interpretation by the reviewer and so many basic problems are discussed, such as that of the origin of metamery, the significance of function for phylogenetic interpretations, and the effects of one organ system on others, that it becomes of considerable interest to the student of phylogeny and evolution.

An Italian biosystematics.[6] Two Italian biologists have joined to write an account of the theory and the practices of systematics. S. Beer, an entomologist, contributes chapters on the history of systematics, on taxonomic characters, on taxonomic categories, and on problems of terminology and nomenclature. The treatment is based on the current literature, often illustrated by situations among the Lepidoptera, personally known to the author. It is a readable and competent treatment. The second part of the volume (pp. 323–550) by A. Sacchetti, an anthropologist and statistician, deals with the biometrical treatment of populations and taxonomic categories. A series of magnificent color plates illustrates sibling species, geographic and individual variation, particularly among the lepidopterans.

Fortuitous polymorphism?[7] Lamotte's long awaited monographic study of variation in the French populations of the snail *Cepaea nemoralis* is now available. It is based on a study of more than 100,000 specimens from nearly 1,000 colonies. The study contains a wealth of information, partly confirming the results of earlier authors, partly extending and partly contradicting them. In the first part of the work (pp. 1–121) the biology of the snails is treated, their population structure, their general variability and what is known of the genetics of their variation. Ninety per cent of the colonies comprise between 500 and 3,000 individuals, but a few large ones exceed 10,000. There is random mating of the various genetic types within each colony. The average distance an individual moves between birth and breeding is 15 meters, which means that linear colonies extending more than 52.5 meters and round colonies covering more than 1,800 square meters are no longer strictly panmictic. Indeed an analysis of one of the larger colonies indicates a definite amount of genetic heterogeneity: If the colony is divided into squares of 10 meters, samples from squares 50 meters apart are twice as different than samples from adjacent squares while samples taken 80 meters apart are three times as different.

The character "unbanded shell" is selected for a detailed analysis (pp. 123–224). It is here that Lamotte comes to results that are somewhat opposed to the conclusions of Taylor, Boettger, Cain and Sheppard, and Schnetter, who believe that the gene controlling this banding has considerable selective significance. Lamotte, although admitting the presence of very slight selective forces, attributes the genetic composition of most populations essentially to mutation (and back mutation), migration, and accident. It would be interesting to find the reasons for this discrepancy of results. It may be a matter of methods. Boettger, Schnetter, and Cain and Sheppard have made very detailed and intensive analyses of a few colonies, the ecology and microclimate of which are well known. Lamotte's method involves the simultaneous analysis of dozens, or hundreds, of colonies. Furthermore, the "unbanded" type may be a heterogeneous class. Cain and Sheppard found that the type "unbanded red" reaches a maximum in old beech forests and "unbanded yellow" in short grass pastures, two diametrically different habitats. The fact that there are greater differences between small colonies than between large ones is ascribed by Lamotte to hazard (p. 152). It seems to me, however, that with the reduced heterozygosity of small colonies the effects of selection will be more immediately apparent. Also, small colonies will occupy more uniform habitats. It would seem

[5] Weber, H. 1952. Morphologie, histologie und Entwicklungsgeschichte der Articulaten. Fortschr. Zool., N. F., **9**: 18–231.

[6] Beer, S., and A. Sacchetti. 1952. Problemi di sistematica biologica. Edizioni Scientifiche Einaudi, 671 pp.

[7] Lamotte, M. 1951. Recherches sur la structure génétique des populations naturelles de *Cepaea nemoralis* (L.). Suppl. 35 au Bull. Biol. France et Belg., 239 pp.

entirely possible to explain this difference between large and small colonies in terms of selection.

There is virtually no correlation between percentage of banding in *Cepaea nemoralis* and the closely related and very similar *C. hortensis* in areas where both species overlap. This independence of variation indicates that predator selection is only of minor importance.

One consideration, neglected by most authors, is that of the wide distribution of banding among land snails. There are dozens, if not hundreds, of species in many genera showing similar variation. One has the impression that a basic polymorphic mechanism is involved, as in the avian and mammalian blood groups, the genes of which can become associated with all sorts of physiological viability factors. A statistical analysis of phenotypes, which lumps the dominant homozygotes with the heterozygotes and which neglects the genetic background on which these genotypes are placed, is perhaps an entirely unsuitable method of analysis.

Although some of Lamotte's conclusions may have to be revised, he has brought new methods and new viewpoints to the ever fascinating problem of the banded snails. His study is a major contribution.

Genetic differences between human isolates.[8] Whether and to what extent accidents of sampling have evolutionary effects are questions of considerable importance, which are not yet answered with unanimity. Every new investigation of the problem is therefore welcome, particularly if it presents clearcut facts. Glass and his co-workers present genetic data on members of a religious sect which lives in the same physical and cultural environment as the rest of the population but intermarries with outsiders only to a limited extent. The effective size of this population is about 90. It is found that at five of seven studied loci the gene frequencies differ significantly from those of the U. S. white population and from the West German population (from which the isolate was originally derived). This difference is ascribed to genetic drift, contributed by three factors: "(a) the accidental composition of the original community . . . ; (b) the effects in each generation of the random sampling of gametes in a very small population; and (c) the chance exclusion of genes borne by those who leave the community" (about 25 per cent of each generation). The contribution of these factors to the observed deviations of the gene frequency are undeniable, but it still remains an open question whether the isolate would have maintained itself sufficiently long to permit fixation. The effect of the differences of the genetic background is not discussed nor the probable physiological effects of the genes which produce the observed phenotypic manifestations.

Geographic and seasonal variation in weasels.[9] Hall's excellent monographic revision of the American weasels contains a wealth of interesting information, biological and systematic. In the northern part of the ranges of each of the three North American species of weasels, a white winter coat is assumed, known as ermine. In the more southern portion of the range the fur is brown in both seasons, and there is a belt (illustrated by a map) inhabited by populations in which some individuals molt into the white coat, others do not. It would be interesting to correlate this with a map showing the average number of days in which the ground is covered by snow. Whether or not a weasel molts in fall into the white coat is genetically determined, but the time of the molt is determined by an interaction of environmental (*e.g.*, light) and endocrine factors. Even in the brown coat there is a close correlation between coat color and climate. The upper parts are blackish brown in *M. frenata* from humid tropical Panama and pale brown in the subspecies from arid New Mexico. A colored plate shows this correlation between rainfall and coloration for ten subspecies. When Hall began his studies in 1925, 29 full species of American weasels were recognized. They are now reduced to 4 species (with 68 subspecies), figures which illustrate graphically the modern trend toward comprehensive, polytypic species.

Stored genetic variability.[10] Classical Mendelian genetics specialized in the analysis of single gene loci. When it was realized that a single character may be affected by several, if not scores or hundreds of genes, it became necessary to add new methods of analysis. Among these the method of testing whole chromosomes, developed by Muller and others, proved particularly productive. It permits testing stocks that are homozygous for certain chromosomes, as well as heterozygous for known combinations. Of four wild chromosomes of *Drosophila melanogaster*, three differed significantly from each other in their effect on abdominal chaetae. When these lines were made homozygous they did not respond to selection for increased or decreased bristle number during the 8–11 generations of the experiment (with one exception caused by extrinsic factors). If a heterozygous pairing of two

[8] Glass, Bentley, *et al.* 1952. Genetic drift in a religious isolate. Amer. Nat., **86**: 145–159.

[9] Hall, E. Raymond. 1951. American Weasels. Univ. Kansas Publ., Mus. Nat. Hist., **4**: 1–466, 41 plates, 31 figs.

[10] Harrison, B. J., and K. Mather. 1950. Polygenic variability in chromosomes of *Drosophila melanogaster* obtained from the wild. Heredity, **4**: 295–312.

of these chromosomes was effected (with the remainder of the chromosomes held constant), a population was started with a new compound chromosome (owing to crossing over) which responded more or less markedly to selection. The new combination of genes contained sufficient genetic variability to permit relatively rapid increase and decrease of the number of chaetae by 25 per cent. It is implied, but not insisted upon, that this variation is due to some major genes and numerous polygenes.

Quantitative inheritance.[11] The whole problem of the nature of quantitative inheritance is considered by Robertson and Reeve in the general discussion of a set of experiments dealing with body size in *Drosophila*. In particular, they question whether it is justified to distinguish between oligogenes and polygenes. Indeed much of the evidence accumulated within recent years indicates that the total genetic background severely affects the phenotypical expression of most genes placed on it. Reciprocally, the chemical products of a given gene may affect to varying degrees various developmental processes in different parts of the body. Instead of having two neatly separated classes of genes—oligogenes producing the major effects, and polygenes modifying the expressivity of the oligogenes—every gene might have major "oligogenic" and minor "polygenic" effects. The same gene then would be an oligogene or a polygene depending on which of its pleiotropic effects is studied.

Mather's former emphasis on polygenes has had a very wholesome effect by bringing out what a special group the "Mendelian" genes are with which most genetic work in the past had been conducted. Now that this point is generally accepted, it might be useful to go still one step farther and consider every character as the product of an intricate interaction of genes, rather than the product of *a* gene (and *its* modifiers) or of a few oligogenes with their polygenes.

Populations and evolution.[12] Dobzhansky gives here a short but particularly lucid exposition of some of the findings and concepts of population genetics. The significance of the difference between sexual populations and asexual clones, the various orders of populations, mechanisms to increase the fitness of populations and to improve their ecological tolerance, and finally the meaning of species and of speciation are discussed.

Speciation in birds.[13] A survey of the literature on species and speciation in birds published since 1939, with particular emphasis on ecological factors.

Species recognition.[14] Males of several species of butterflies, particularly *Pieris napi*, were given the choice of dummies with the outline of females. In nearly all cases the dummy that most resembled the female (white in the case of *P. napi*) attracted the males most strongly. White (= *napi*-like) dummies were more attractive to males of *P. bryoniae* than yellowish dummies colored like their own females. This sexual selection in favor of white females is evidently overruled by selection for viability factors associated with the genes producing the normal female coloration of *bryoniae* females.

Polyploidy in a turbellarian.[15] A blind, white cave (or spring) turbellarian of the Swiss Alps, *Dendrocoelum infernale*, with $n = 16$ is exceedingly similar to *D. lacteum* ($n = 8$), except for the lack of eyes. Author interprets this hermaphroditic species as an autopolyploid of *D. lacteum*. There are various physiological differences between the species, such as temperature preference and resistance to various poisons.

Stabilized hybrid populations and gene complexes.[16] Three morphological genera of cyprinodonts occur in Anatolia (Turkey); the species in one (*Aphanius*) are normally scaled, in the two others scaling is either more or less reduced (*Anatolichthys*) or virtually absent (*Kosswigichthys*). Interspecific and intergeneric crosses among these forms are usually fertile, even between such that are sympatric, except when *Kosswigichthys* is involved. As to be expected, when a scaled population is crossed with another scaled population, the F_1 is scaled, and when a member of a scaleless population is crossed to a member of another scaleless population, the offspring is scaleless. But there are interesting exceptions. In crosses of three scaled populations the offspring was largely scaleless, in another cross most of the offspring was scaled, even though on the basis of the constitution of the parents a scaleless F_1 would have to be expected.

It is thus evident that the recombination of gene complexes resulting from interpopulation

[11] Robertson, F. W., and E. Reeve. 1952. Studies in quantitative inheritance. I. The effects of selection of wing and thorax length in *Drosophila melanogaster*. Jour. Genetics, **50**: 414–448.

[12] Dobzhansky, Th. 1950. Mendelian populations and their evolution. Amer. Nat., **84**: 401–418.

[13] Mayr, E. 1951. Speciation in birds. Proc. Xth Int. Ornith. Congress, Uppsala, pp. 91–131.

[14] Petersen, B., O. Törnblom, and U. O. Bodin. 1952. Verhaltungsstudien am Rapsweissling (*Pieris napi*) und Bergweissling (*Pieris bryoniae*). Behavior, **4**: 67–84.

[15] Aeppli, E. 1952. Natürliche Polyploidie etc. Z. Vererbungslehre, **84**: 182–212.

[16] Aksiray, F. 1952. Genetical contributions to the systematical relationship of Anatolian Cyprinodont fishes. Publ. Hydrobiol. Res. Inst., Univ. Istanbul, Ser. B, vol. **1**: 33–81.

crosses often produces unpredictable results. Back crosses and other additional genetic analysis indicate that the genetic basis of these characters is highly multifactorial. Further analysis indicated that the populations of the so-called genus *Anatolichthys* have all the characteristics of stabilized hybrid populations between *Aphanius* and a *Kosswigichthys*-like ancestor. There is no sexual isolation between any species of *Aphanius* and the only living species of *Kosswigichthys*, but nearly all hybrids, so far bred, were sterile in spite of their high viability. A few fertile F_1 females produced only sterile males in back crosses. The phenotype of the hybrid is consistent with the theory of the hybrid origin of *Anatolichthys*. The parallelism between hybridism in relic streams in the deserts of Anatolia and the American West is remarkable. Fertility, however, seems greater in the Anatolian group.

Meristic characters and environment.[17] Work on the sea trout (*Salmo trutta*) extends the findings of earlier authors that by heat or cold treatment "phenocopies" of different natural populations may be obtained. The vertebrae number of a "cold treated" warm water sample was 58–62, which is like that of Scandinavian populations; in a "warm treated" cold water sample it was 55–59, which is much like a South European population (53–59). Characters laid down early in development, such as number of vertebrae, expressed under constant conditions more clearly genotypic differences than late developing characters, such as number of dorsal fin rays. Some chemical factors, like salinity and oxygen content of the water, also affect meristic characters. Author emphasizes that a great deal more work needs to be done to determine what part of the meristic characters, that are used so much in fisheries research, have a genotypic basis.

Sympatric hybridization.[18] Two species of Malaysian Kingfishers (*Ceyx rufidorsus* and *C. erithacus*) hybridize freely in their rather extensive area of overlap. This fact was discovered by Ripley and is confirmed by Voous. Among 72 Sumatran specimens there were 35 per cent hybrids, among 89 specimens from the Bornean area there were 58 per cent hybrids. It is difficult to understand what prevents the complete merging of the two species, in view of this high frequency of hybridization.

Population structure in birds.[19] It is now generally acknowledged that certain features of populations are of decisive importance for rates and directions of evolutionary change. Unfortunately, most of our knowledge of population phenomena is derived from laboratory or otherwise artificial populations. David Lack, who has been a leader in the study of populations of birds, has prepared a valuable review of the work done on bird population from 1938 to 1949. Density dependent factors are very apparent. There is evidence of a good deal of "overproduction" of young normally, and after heavy decimations populations usually return rather quickly to their "normal" density, which fluctuates within prescribed limits. Annual mortality of adults is about the same in every age group, and extremely few birds reach an age level where they might die of "old age." In most passerine birds some 42–65 per cent of each year class die annually, the averages differing between species and localities. Predation appears to be an important mortality factor among gallinaceous and passerine birds. Available food supply during a critical period of the year seems to be involved—directly or indirectly—in most of the residual mortality.

Studies of this sort are particularly stimulating as bringing out the interaction of many conflicting factors and by showing how mortality factors influence indirectly family structure, habitat selection, feeding plasticity and many other variable behavior elements that can be modified by selection.

Ecotypes and range changes.[20] The conclusion that most species consist of numerous genetically and ecologically different local populations casts new light on the problem of range changes. Range expansions usually do not affect the species as a whole, but are local phenomena of specific peripheral populations which are genetically and ecologically preadapted to take advantage of slight changes in the physical or biotic environment. The relative share of the intrinsic (= gene environment) and extrinsic (= environmental changes) factors can at best be only estimated. Author illustrates his discussions by numerous distributional phenomena.

Climatic changes and evolution.[21] A group of Finnish climatologists, geographers and biologists arranged an important symposium on climatic changes in Finland during the past 100 years. There have been decided fluctuations,

[17] Taning, A. V. 1952. Experimental study of meristic characters in fishes. Biol. Rev., **27**: 169–193.

[18] Voous, K. H. 1951. Distributional and evolutionary history of the Kingfisher genus *Ceyx* in Malaysia. Proc. Xth Int. Ornith. Congress, Uppsala, pp. 177–183.

[19] Lack, D. 1951. Population ecology in birds. A review. Proc. Xth Int. Ornith. Congress, Uppsala, pp. 409–448.

[20] Voipio, P. 1952. Oekogenetische Differenzierung und Populationsdynamik. Ornis Fennica **29**: 1–26.

[21] Hustich, I. (ed.). 1952. The recent climatic fluctuation in Finland and its consequences. Fennia, **75**, 128 pp.

different for every month of the year. For most months there has been a temperature minimum 1850–1880 and a maximum 1930–1940. This has resulted in many range changes, retreats of northern species and advances of southern species. The resulting shifts of selection pressure are complex and not easily analyzed; an improvement of the climatic situation, for instance, may favor a predator even more than its prey.

Pigment and climate.[22] A careful biometrical analysis of the size of the black, yellow and red pigment areas on the wings of the butterfly *Melitaea chalcedona* in California shows that many of the 30 sampled populations differ from each other significantly. The amount of red increases particularly strikingly in the desert district. No reason could be found why some populations are highly variable, as for instance those of isolated mountain populations in the Mohave desert area. Most of the observed variation is undoubtedly genetic since the adults were raised in the laboratory from wild collected larvae.

Adaptive evolution in the reproduction of marine bottom invertebrates.[23] Though written as "ecology" the material of Thorson's review is of first rate importance to the evolutionist. Every step in the development of the larvae from fertilization to adulthood is subjected to strong selection pressures which have resulted in manifold adaptive devices. About 70 per cent of the bottom invertebrates have a plankton feeding pelagic larval stage during which enormous mortality occurs. A single individual of the mollusc *Aplysia californica* spawns 480 million eggs in less than 5 months. If there is non-pelagic development, eggs with much yolk, brood protection, and vivipary, the number of eggs is drastically reduced. Thorson gives a detailed analysis of the modes of spawning and fertilization, types of larval development, and sources of loss during pelagic development, and how these phenomena are correlated with geographical and ecological distribution. The arctic, antarctic, and deep seas have bottom waters with low temperatures and poor food conditions; as a result only few species there have pelagic larvae. Most interesting are the species that vary their developmental pattern according to the waters in which they occur. In many species there are various isolating mechanisms and other mechanisms reducing the waste of gametes (pp. 6–7).

Dispersal.[24] Marked individuals of a population of prairie deermice (*Peromyscus maniculatus bairdii*) showed a strongly skewed dispersal pattern. There are indications of three types of individuals, those that stayed in the vicinity of the birthplace, those that moved a short distance (150–750 feet), and those that moved long distances (several thousand feet). The long distance travelers, which have also been recorded for many other species, are of special importance as causing a high rate of gene flow.

[22] Le Gare, M. J., and W. Hovanitz. 1951. Genetic and ecologic analyses of wild populations in Lepidoptera. II. Color pattern variation in *Melitaea chalcedona*. Wasmann Jour. Biol., **9**: 257–310.

[23] Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev., **25**: 1–45.

[24] Dice, L. R., and W. E. Howard. 1951. Distance of dispersal by prairie deermice from birthplaces to breeding sites. Contr. Lab. Vertebrate Biol., **50**: 1–15.

DARWIN'S JOURNAL[1] AND OTHER PUBLICATIONS

EDWIN H. COLBERT

A recently published book of particular interest to evolutionists is a facsimile reprint of Darwin's journal of his voyage on the *Beagle*, brought out by the Hafner Publishing Company of New York and London. This is a large and handsome volume, printed by the offset process.

The first edition of Darwin's journal was actually the third volume of a narrative account of the *Beagle* expedition, the first two volumes having been prepared by Captains Fitzroy and King. It appeared in 1839. Darwin's journal was at that time published independently by Messrs. Colburn, some copies of which were dated 1839 and some 1840. It is this original edition of Darwin's journal as an independent work, now very rare, that has been reproduced. The Journal was published again as a second edition "corrected with additions" in 1845, while it appeared in still a third form in 1860 under the title of "A Naturalist's Voyage." These

[1] Journal of Researches into the Geology and Natural History of the Various Countries visited by *H. M. S. Beagle*. By Charles Darwin. 1839. Facsimile reprint of the first edition. Hafner Publishing Company, New York-London. 615 pp. 20 plates, frontispiece. 1952. $7.50.

two later editions are the ones commonly available at the present time as reprints.

This facsimile reprint includes, in addition to the full text, reproductions of the figures that appeared in the first edition, and also sixteen plates from the King and Fitzroy volumes. For a frontispiece there is a diagram of the *Beagle*, as drawn by Captain King many years after the voyage, and first published in 1890.

The following volumes deserve notice, although they are not reviewed here, since they are not concerned with evolutionary problems.

Carr, Archie. 1952. Handbook of turtles. Comstock Publishing Associates—A Division of Cornell University Press, Ithaca, New York. 542 pp. 37 figs. 82 plates.

Dowdeswell, W. H. 1952. Animal ecology. Methuen & Co., Ltd., London. 207 pp. 45 figs. 16 plates.

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